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目　　次

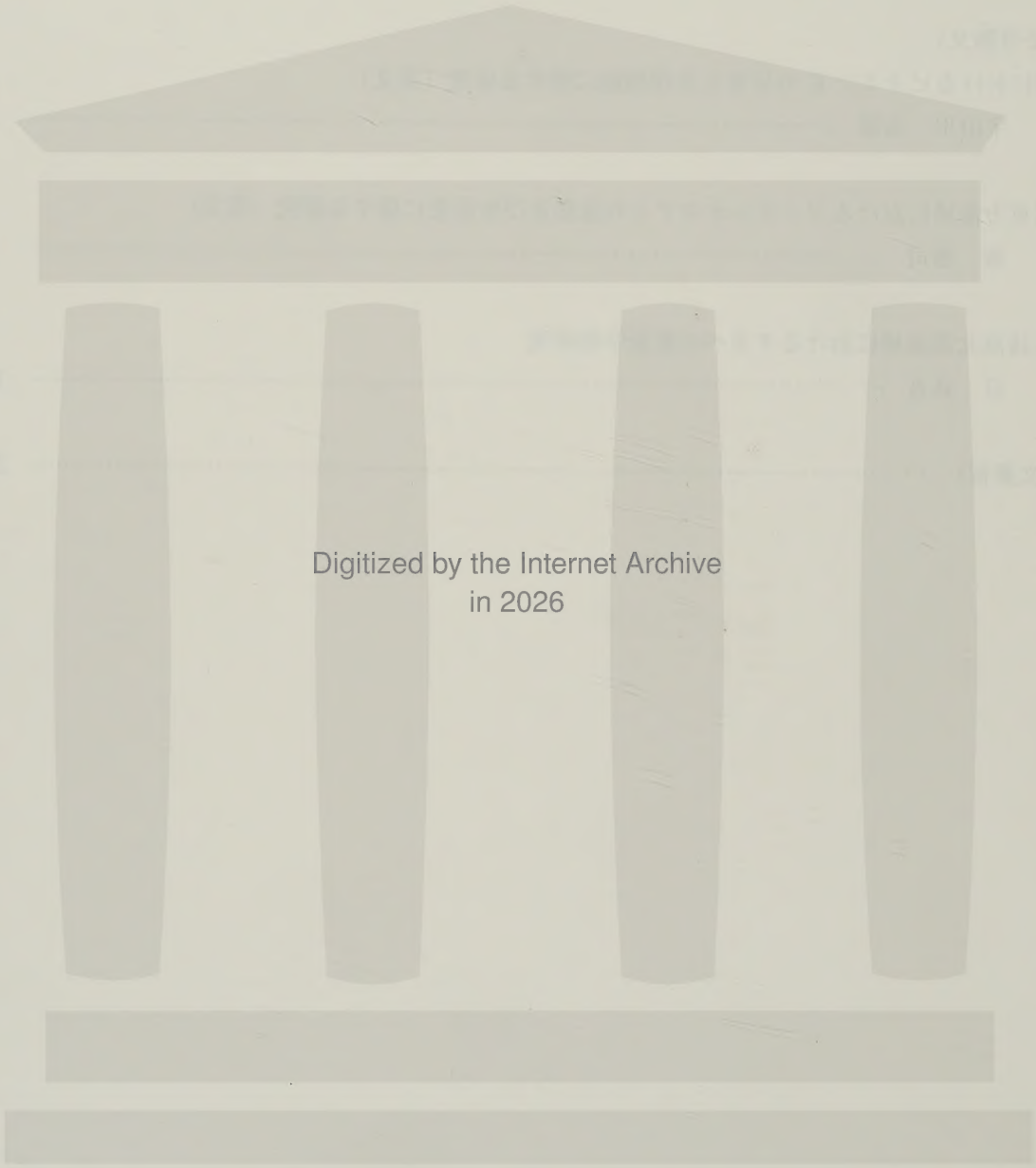
（博士号論文）

魚類におけるビタミンＫの分布と生理機能に関する研究（英文）
　　宇田川　美穂 …… 1

本州東方海域におけるツノナシオキアミの漁業及び生活史に関する研究（英文）
　　瀧　憲司 …… 41

伊豆諸島北部海域におけるタカベの資源学的研究
　　亘　真吾 …… 167

（和文要旨） …… 243



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博士号論文

Studies on the Distribution and Physiological Function of Vitamin K in Fish [*1]

Miho Udagawa [*2]

Abstract: Basic information on the distribution and role of vitamin K in fish was studied in relation to dietary intake.

Chapter 1 describes the concentrations of phylloquinone (PK) and menaquinones (MKs) in various tissues of wild and cultured fishes as the results of analysis based on the HPLC method. The major vitamin K in wild pelagic fish was PK, and the stomach and intestinal contents of pelagic fish showed much higher levels of PK than MK-4. Demersal fish contained relatively large amounts of MK-4 and PK but only small amounts of long chained MKs. In demersal fish, the contents of the gastrointestinal tracts were rich in MK-long chains. However, a discrepancy between the composition pattern of vitamin K in the tissues and contents of the gastrointestinal tract was observed. Cultured fish fed a menadione (MD) supplemented feed were rich in MK-4, which indicates that MD was converted to MK-4 in the body. From these results, it was concluded that either PK or MK-4 deposited in the body originates from their food and stored mainly in the liver, and the different forms of vitamin K are absorbed and/or accumulated in the tissues based on different physiological pathways.

In Chapter 2, the contents of vitamin K in the plasma and tissues (kidney, liver and gonad) of fish fed diets supplemented with different vitamin K groups were determined. The PK rich diet raised the PK concentration in the plasma and the tissues much higher than the diets supplemented with short and/or long chain MKs. This indicates that PK is more easily accumulated into the body of fish than the MK homologues.

Chapter 3 describes the effect of different dosages of vitamin K, either as PK or menadione sodium bisulfite (MSB), on mortality and vertebral formation. Rearing during the spawning season with a vitamin K free diet for 11 weeks, led to most of the male fish dying. In the kidney tissue of the fish fed with a vitamin K free diet, a large number of immature erythrocytes was observed. This indicates that the female fish had been affected by hematoporia and/or hematopoiesis brought about by a deficiency in vitamin K. Diets without vitamin K caused a significantly higher incidence of bone deformity in larvae than diets supplemented with vitamin K. The maternal effect of PK deficiency on bone structures was examined in the larvae. The vitamin K deficient larvae had an abnormal vertebral formation, while PK rich larvae showed a low rate of abnormality. When fed the vitamin K deficient diet, larvae which had been fed the vitamin K rich and deficient diets had a both high rate of abnormality after 30 days, with only larvae which wrere hatched from vitamin K rich eggs and then fed on a vitamin K rich diet showed a low rate of abnormality. These results indicate that vitamin K deficiency affects bone structure both in early development and during growth.

In Chapter 4, the effect of PK on the bone structure in fish was observed histochemically. The bone structure of vitamin K deficiency larvae was thin and rough after the feeding experiment for 30 days. It seemed to be connected after fine fracture of a bone surface. In

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contrast, in larvae fed a PK rich diet this phenomenon was not observed. These results imply that vitamin K deficiency induced bone abnormality with thin and weak structure. A vitamin K rich diet increased the osteoblast-like cells. These results imply that PK is necessary to activate the osteoblasts. It is indicated that at least part of the effects of PK on bone resorption may regulate the osteoblasts activity through an unidentified mechanism.

In Chapter 5, a comprehensive discussion is given of the all results and conclusions so far described.

Key Words: phylloquinone, menaquinone, tissue distribution, vitamin K deficiency,,

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Contents

Introduction
Chapter 1. Distribution of vitamin K in fish
1.1. Tissue distribution of phylloquinone and menaquinone-4 in fish
1.2. Difference in the distribution of vitamin K with feed habitat in fish
1.2.1. Content of phylloquinone and menaquinone derivatives in the organs of pelagic and demersal fishes
1.2.2. Comparison of the composition of vitamin K in different forms between cultured and wild fish

Chapter 2. Absorption of vitamin K in fish

Chapter 3. Physiological function of vitamin K in fish
3.1. Physiological abnormality and the tissue vitamin K level in the fish fed with a vitamin K free diet in fish
3.2. The effect of dietary vitamin K (phylloquinone and menadione) levels on the vertebral formation in fish
3.3. The maternal effect of phylloquinone deficiency on bone structure in fish

Chapter 4. Histochemical study of the effect of vitamin K on fish bone
4.1. Histochemical study of the effect of vitamin K on bone development
4.2. Histochemicl characteristics of the osteoblastic cells in fish fed a diet with vitamin K

Chapter 5. Comprehensive Discussion

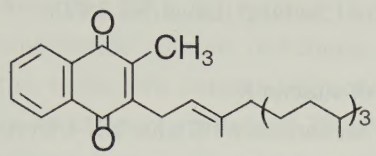
Chapter 6. Summary

Acknowledgements
References

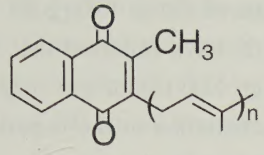
Introduction

Vitamin K was first discovered by Dam (1935) as a substance playing an important role in the synthesis of blood-clotting factors. Vitamin K is a group name for a series of related compounds that act as a cofactor for the microsomal enzyme γ-glutamylcarboxylase. This enzyme is involved in the post-translational conversion of peptide-bound glutamate residues into γ-carboxyglutamate (Gla), which occurs in a number of blood coagulation factors and bone proteins (Furie B. and Furie B. C. 1988; Hauschka *et al.* 1989; Vermeer 1990). Furthermore, a variety of diseases due to vitamin K deficiency has been reported in mammals. In particular, a few week old human infants are prone to hemorrhage due to vitamin K deficiency. Attention has been increasingly focused on the importance of vitamin K for normal bone development. However, the role of vitamin K in fish has not been well documented. In this study, the physiology, distribution and absorption of vitamin K in relation to the intake of vitamin K in fish is described.

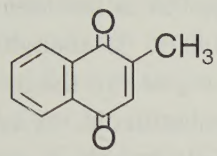
There are several derivatives of vitamin K as follows: 1) phylloquinone (PK) called vitamin K1, is produced by plants; 2) menaquinone (MK) which is synthesized by microorganisms is called vitamin K_2 and has long side-chains arranged in MK-n series. MK-4 consists of short isoprene units and MK-9 is one of a typical long-chain MK produced



Phylloquinone (K_1)



Menaquinone-n (K_2)



Menadione (K_3)

Fig. 1. Chemical structure of vitamin K.

by bacteria; 3) Synthetic analogues of menadione (MD) designated as vitamin K_3 have no side-chains, and are utilized for animal and fish commercial diets (Fig. 1). Water-soluble salt of synthetic menadione, menadione sodium bisulfite (MSB) is generally supplemented in commercial fish diets. Parts of PK, MK and MD are metabolized to MK-4 in the tissues (Billeter *et al.* 1964). Therefore, as basic information on the utilization of vitamin K, the distribution of the various forms of vitamin K in tissues and origins were determined.

There are many reports on vitamin K requirements for mammals except for fish, and vitamin K is generally considered to be an essential nutrient for mammals. Woodward (1994) gave quantitative estimates of the dietary requirement of vitamin K for salmonids. Poston (1964) reported that in the brook trout blood coagulation time was delayed and the microhematocrit value decreased by vitamin K deficiency, but that the growth rate was not appreciably affected. Kitamura *et al.* (1967) also reported that in the rainbow trout, vitamin K deficiency was associated only with anemia. As for the catfish, no symptoms of vitamin K deficiency were observed (Murai and Andrews 1977). On the other hand, Taveekijakarn *et al.* (1996) reported that the mortality level in vitamin K deficient amago salmon reached 50% and the histopathological changes were detected.

The physiological function of vitamin K was originally thought to be limited to the role of cofactor in blood coagulation. Recently, the important role of vitamin K in normal bone development has been revealed in mammals (Vermeer *et al.* 1996; Shearer 1996). Residue-specific carboxylation of proteins is one of the functions of vitamin K and calcium-binding proteins such as osteocalcin and matrix-Gla protein also require vitamin K for their carboxylation. Thus, the importance of vitamin K in mammalian bone development has attracted the interest of many researchers (Kohlmeier *et al.* 1996), while the participation of vitamin K in fish bone development has not been investigated.

In this study the effect of vitamin K deficiency on fish mortality and bone development are described.

Chapter 1. Distribution of vitamin K in fish

Vitamin K is essential for the synthesis of clotting factors in the liver of mammals. Its metabolic role also has been more clearly defined than that of the other three fat-soluble vitamins, even though it was the last of the fat-soluble vitamins to be discovered (Suttie 1980; Korman and Weiser 1983). Many types of compounds such as PK, MKs and MD exhibit vitamin K activity. In terrestrial mammals, long chain MKs (MK-5 through MK-13) are usually synthesized by the intestinal bacteria and PK comes from food being consumed (Will *et al.* 1992). On the other hand, information on the physiological roll of vitamin K is limited in fish, and even its essentiality for fish is not well established yet among fishes (Murai and Andrews 1977; Kawatsu and Ikeda 1988; Kawatsu *et al.* 1989). In this chapter, distribution of vitamin K especially difference by food habitat in fish is described.

1.1. Tissue distribution of phylloquinone and menaquinone-4 in fish

More basic information, such as the distribution of various forms of vitamin K in tissues and those origins are necessary as the first step to elucidate the physiological roles of vitamin K in fish. In

this section, the author attempted to measure the concentrations of PK and MK-4 in various tissues of fish with a HPLC method modifying the sample preparations. Using these techniques, the author determined distribution of PK and MK-4 in various tissues of wild sardine *Sardinops melanostictus* feeding on PK-rich phytoplanktons such as diatoms and cultured sardine fed MD-supplemented feed to determine the origin of these compounds.

Materials and Methods

Materials

Cultured sardine was raised in a $20m^3$ round tank at National Research Institute of Aquaculture. A commercial trout feed supplemented with MSB was fed to the fish at a daily rate of about 2% of biomass for one year. Five fish were randomly sampled and immediately frozen after the blood sample was collected from the caudal vein. The first lot of wild sardine (wild sardine 1) were purchased from the Tukiji fish market on Nov. 1991. They were kept in ice after captured at unknown area and were still extremely fresh condition. Five fish having a similar body length to the cultured fish were selected but the blood sample was not available. The second lot of wild sardine (wild sardine 2) were caught in the Pacific Ocean approximately 90km off Shionomisaki, Japan, by angling from the research vessel Soyo Maru on Feb. 23 1992. They were kept at −80℃ immediately after being caught but the blood was not sampled. The stomach contents and intestinal contents were separately collected from wild sardine 2. Planktons were collected with 100 μm mesh NORPAC net by vertical tow (0-150m) simultaneously at the same area where wild sardine 2 were angled. The gonad somatic index (GSI) was calculated as follows: GSI=GW×100/BW, where GW and BW represent gonad weight (g) and body weight (g).

Chemicals

Standard PK and MK-4 were purchased from Sigma Chemical Co. (St Louis, MO). The hexane, methanol and ethanol were of HPLC grade and purchased from Wako Pure Chemical Industries, LTD. Frolisil (100-200mesh) was also product of Wako Pure Chemical Industries, LTD.

Analysis of vitamin K

In this section, only PK and MK-4 were measured because no rich source of typical vitamin K synthesizing microorganisms has been described in the intestine of cultured fishes (Margolis, 1953) and also Will *et al.* (1992) have reported that long chain MKs (MK-5 through MK-13) of gut origin make a relatively minor contribution to the hepatic stores of vitamin K in rats and chicks.

The samples of heart, kidney, muscle and serum were prepared with Sep-Pak as has been described by Nagaoka *et al.* (1989). If enough quantity was available, about 1 g of the tissue was used but otherwise used whole tissue. A sample was homogenized with 1 ml of distilled water and 4 ml of ethanol. Then 6 ml of *n*-hexane was added. And the mixture was shaken for 5min, followed by centrifugation at 800*g* for 5min. A 5ml portion of the upper layer was transferred into a centrifuge tube and evaporated. The residue was dissolved in 2 ml of *n*-hexane. A silica Sep-Pak cartridge (Waters) was washed with 10ml of *n*-hexane/ether (93/7) and 10ml of *n*-hexane. The sample was loaded, washed with 10ml of *n*-hexane, and eluted with 5ml of *n*-hexane/ether (93/7). This eluate was evaporated and dissolved in 0.2ml of ethanol.

The liver sample was applied to frolisil column prior to the Sep-Pak treatment in order to remove various compounds which was found only in the liver and affected the reading. The frolisil was washed with *n*-hexane, packed into a glass column (5mm (i.d.)×60mm), and washed with 10ml of *n*-hexane. The residue from the silica Sep-Pak cartridge was dissolved in 0.2ml *n*-hexane and loaded, washed with 10ml of *n*-hexane, eluted with 10ml of *n*-hexane/chroloform (60/40). This eluate was evaporated and dissolved in 0.2 ml of ethanol.

The total sample completed these procedures was injected into the HPLC system. MSB was measured by an ordinary method (Chiba, 1985). All chamical analysis was conducted under the absence of daylight by using brown glassware.

HPLC system

The HPLC system consisted of a Hitachi L-6000

pump, Lichrospher RP-8 (e) column (4×250mm, 5m), platinum oxide column (4×20mm, EICOM Co.) for the reduction column, Hitachi F-1050 fluorescence spectrophotometer and Hitachi D-2500 chromato-integrator. The mobile phase was methanol containing 2% sodium perchlorate and deaerated by bubbling argon gas. Flow rate was 0.5ml/min. Detection was made fluorometrically at an excitation wavelength of 254 nm and an emission wavelength of 430 nm as described by Shino (1988).

Statistics

Data on the size of fish and gonad somatic index (GSI) were analyzed by Duncan's multiple range and multiple *F*-test (Duncan, 1955). Man-Whitney *U*-test and *t*-test for paired samples were used for the contents of PK and MK-4 in each tissue. The statistical differences between the treatment groups were assessed at a 5% level of probability. The values shown in the text are means ±SEM.

Results and discussion

The physical characteristics of the sardine used for this study were shown in Table 1. Although all fish used in this study had a similar body length, there were significant differences in body weight, liver weight and maturation stage. The GSI clearly indicates, wild sardine 1 were still immature while wild sardine 2 were fully matured and cultured sardine were intermediate. The liver of wild sardine 1 were significantly smaller than those of cultured sardine and wild sardine 2.

As clearly shown in HPLC profile (Fig. 2), identifications of PK and MK-4 peaks became possible by the previous treatment with the frolisil column. Thus, the HPLC method employed can be applicable for determination of PK and MK-4 even for the liver sample if various other compounds were removed in advance by passing through the frolisil column.

The concentrations of PK in the various tissues examined were shown in Fig. 3. PK contents in all tissues of wild sardine 2 were much higher than those of cultured sardine and wild sardine 1, especially in the liver. PK content in the liver of cultured sardine was only 1.65±1.11ng/g of wet tissue which was less than 1/9 of those of wild sardine 1 (14.75±8.23) and wild sardine 2 (46.48 ±10.86). In wild sardine 2, the gonad contained significantly higher level of PK than the kidney and heart (*t*-test for paired sample) but it was about 1/3 in the liver. While appreciable quantity of PK was found only in the liver of wild sardine 1. On the other hands, only fractional quantity of PK was detected among the tissues of cultured sardine including the serum. PK contents in both ordinary and dark muscle were trace amounts in all fish tested.

The concentrations of MK-4 in the various tissues were presented in Fig. 4. MK-4 contents in cultured sardine were significantly higher (at least 2-fold) than those of wild sardine 1 and 2 in all tissues examined except the muscles (Mann-Whitney *U*-test). The highest value (14.20±3.6) was detected from the heart but it was not significantly different from those in the gonad and liver (*t*-test for paired samples). More than 5ng of MK-4 was also found in the kidney and serum. MK-4 concentrations in these tissues of wild sardine 2

Table 1. Physical characteristics of sardine used for determination of vitamin K

	Body length (mm)	Body weight (g)	Liver weight (g)	Condition factor	GSI*
Cultured sardine	200±3.9[a]	129.1±10.8[a]	2.20±0.30[a]	1.62±0.11[a]	2.78±1.85[a]
Wild Sardine 1	192±2.7[a]	100.3±4.7[b]	0.91±0.12[b]	1.41±0.08[b]	0.31±0.16[b]
Wild Sardine 2	296±0.6[a]	101.7±6.1[b]	1.67±0.10[c]	1.36±0.05[b]	8.69±1.57[c]

*Gonad somatic index.
Values are means ± SEM of five fish.
Values in the same column with different superscripts are significantly different (P <0.05).

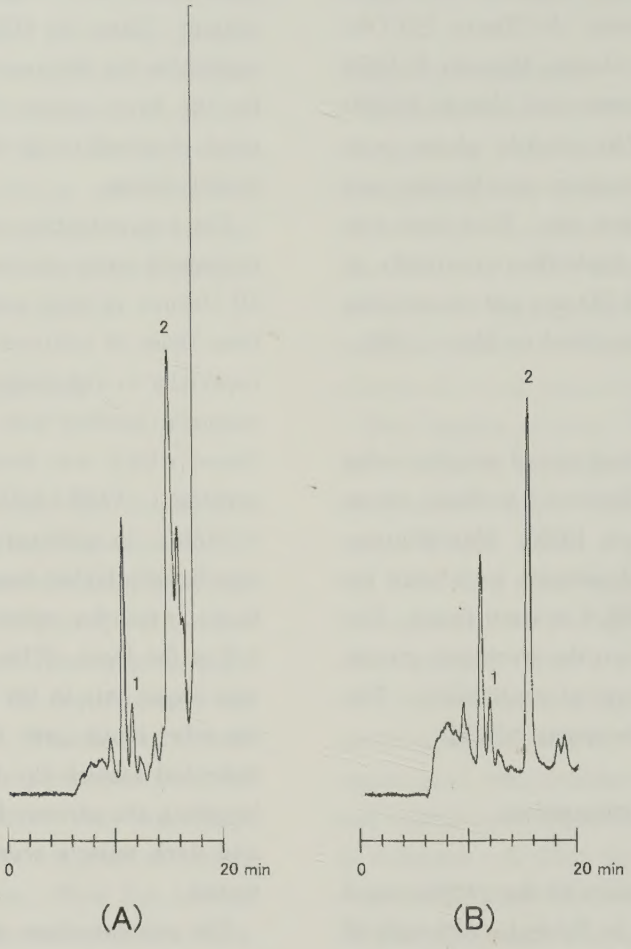


Fig. 2. HPLC separation of vitamin K in liver tissue of sardine. Peak 1 is MK-4, peak 2 is PK. (A): only Sep-Pak was used; (B): Frolisil column was used after Sep-Pak.

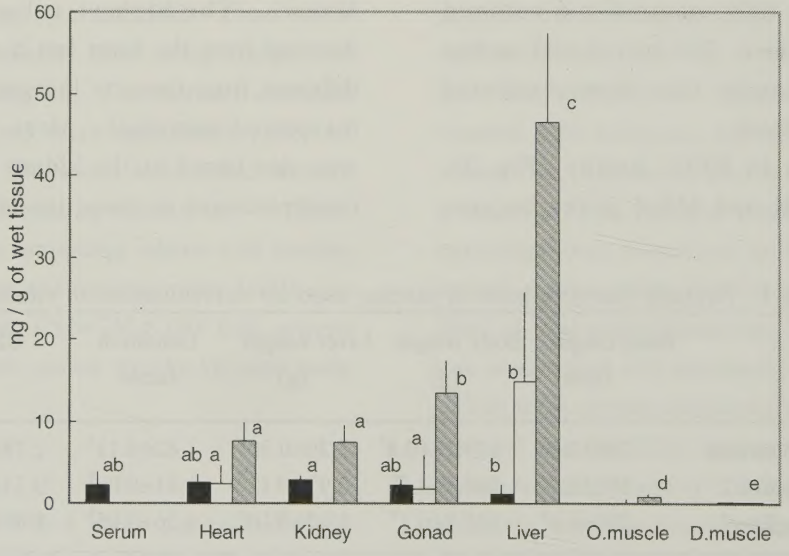


Fig. 3. Phylloquinone contents in various tissues of sardine. Groups of sardine were as follows: solid bars, cultured sardine; open bars, wild sardine 1; hatched bars, wild sardine 2. O. muscle is ordinary muscle and d. muscle is dark muscle. Values in each group with different superscripts are significantly different ($P<0.05$). Values are means ± SEM of five fish.

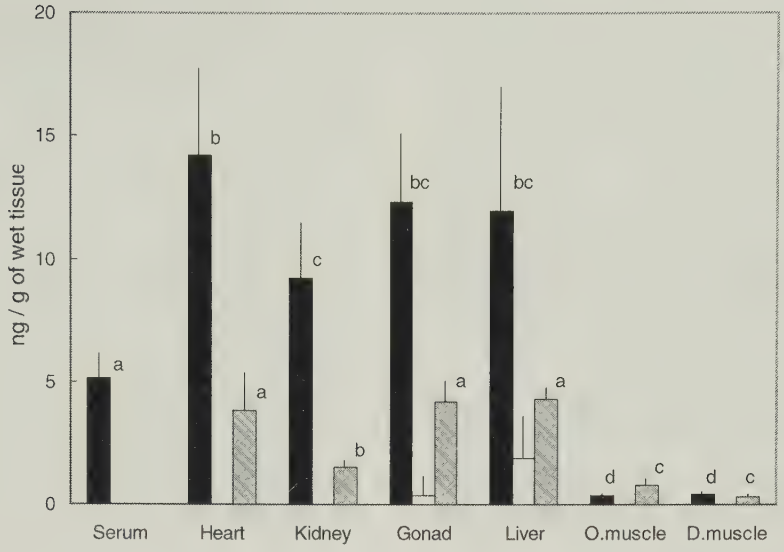


Fig. 4. Menaquinone-4 contents in various tissues of sardine. Groups of sardine were as follows: solid bars, cultured sardine; open bars, wild sardine 1; hatched bars, wild sardine 2. O. muscle is ordinary muscle and d. muscle is dark muscle. Values in each group with different superscripts are significantly different ($P<0.05$) . Values are means ± SEM of five fish.

Table 2. Phylloquinone, menaquinone-4 and menadione contents in food consumed by sardine

	Phylloquinone (ng /g of wet)	Menaquinone-4 (ng /g of wet)	MSB[1)] (ng /g of wet)
Plankton	61	2	-[3)]
Stomach contents*	120±60	12±12	-
Intestinal contents*	160±150	6±5	-
Commercial trout feed	ND[2)]	ND	2.0

*Values are means ± SEM of five specimens.
[1)]MSB: menadione sodium bisulfite.
[2)]ND: not detected.
[3)]-: not measured.

were significantly higher than those of wild sardine 1 but were only comparable values to PK levels in the respective tissues of cultured sardine. Again, the muscle samples contained only trace quantity of MK-4 in all groups.

It is possible that the significant differences in PK and MK-4 contents between wild sardine 1 and 2 were due to the difference in nutritional condition and maturation stage between these two group because the liver weight and GSI were much higher in the latter. Also unknown period of storage in ice can be another factor attributable for the low values in wild sardine 1. Even though these factors were taken into consideration, it can be concluded at least that major vitamin K deposited in the body was PK in wild sardine and MK-4 in cultured sardine.

Analytical results of PK, MK-4 and MSB in the stomach and intestinal contents, planktons which were supposed to be consumed by wild sardine and commercial trout feed which was fed for cultured sardine were shown in Table 2. The planktons contained almost 30 times higher level of PK than MK-4. The stomach and intestinal contents of wild sardine 2 also had at least 10 times higher level of

PK than MK-4. However, no significant difference in both PK and MK-4 concentrations were detected between the stomach and intestinal contents (*t*-test for paired samples). On the other hand, only MSB was found in the commercial feed. These results strongly indicate that vitamin K found in the body of sardine came from food being consumed. Also the lack of any significant difference in MK-4 concentrations between the stomach and intestinal contents suggests that contribution of MK-4 synthesized by intestinal microorganism is minor in sardine. MSB seemed to be converted to MK-4 in the body of sardine as has been well known to take place in the liver of mammals (Billeter *et al.*, 1964) since the commercial trout feed fed for cultured sardine contained only MSB.

More studies are needed to elucidate physiological role of vitamin K in fish. However, the difference in distribution pattern in the tissues between cultured and wild sardine, and its accumulation in the gonad of matured sardine and extremely low concentrations in the muscle could be useful information for this purpose.

1.2. Difference in the distribution of vitamin K with feed habitat in fish

1.2.1. Content of phylloquinone and menaquinone derivatives in the organs of pelagic and demersal fishes

Food habits differ greatly between pelagic fish and demersal fish. Pelagic fish feeds on plankton and small fishes, while demersal fish feeds chiefly on benthos. Benthos are organism which lives in benthic of the sea. Generally, phytoplankton contains a high concentration of PK. On the other hand, it can be assumed that benthos are rich in long chain MKs produced by microorganisms growing on them. This section describes the study to elucidate the relationship between type of vitamin and/or their K levels in various tissues of fish which have the different food habits. The fish species tested were mackerel, *Scomber japonicus* and saury, *Cololabis saira* as pelagic fish examples, and marbled sole, *Limanda yokohamae* and sillago, *Sillago japonica* as demersal fish examples.

Materials and methods

Materials

Mackerel were caught by angling in the Sagami bay, Japan, on 11 February 1993. Saury were also angled in the sea off the Pacific coast of Hokkaido, Japan on 10 September 1993. Marbled sole and sillago were purchased from Kosiba Fishing Port Market in Kanagawa prefecture shortly after being caught at Tokyo bay on 6 November 1993. All the fish samples were kept at −40℃ until used. Five fish of each species were used for analysis. The tissues of heart, kidney, liver, gonad and muscle were separated and the vitamin K content in each specimen was measured, except for the mackerel gonad, because it was not mature. In the cases of mackerel and saury, the muscle tissue was separated further into the ordinary and dark muscles for separate analysis.

The stomach and intestinal contents were collected separately from individual fish. Frozen Pacific krill *Euphausia pacifica* was purchased from Ishinomaki Fishing Port Market in Miyagi prefecture. *Polychaeta spp.* was collected at Kosiba Fishing Port, in Kanagawa prefecture. These materials were also subjected to analysis of vitamin K.

Chemicals

Authentic PK was purchased from Sigma Chemical Co. (St Louis, MO). Authentic MK-4 was kindly provided by Eizai Co. (Tokyo, Japan), and MK-6, 7, 8 and 9 by Nippon Roche Tokyo (Tokyo, Japan). Ethanol, methanol and *n*-hexane, HPLC grade, were purchased from Wako Pure Chemical Industries, (Osaka, japan).

Analysis of vitamin K

PK and MK were measured by HPLC. The tissue specimens were homogenized with a mixture of *n*-hexane, H_2O and ethanol (6:1:4) and shaken for 5min. The solvent extracts were then pre-treated by passing through a Sep-Pak silica cartridge (Waters, Milford, MA) by elution with *n*-hexane and ether mixture. Each eluate was evaporated to dryness under reduced pressure and the residue

was dissolved in 200 μl ethanol (Nagaoka *et al.*, 1989). This solution was used as a sample solution for HPLC analysis. An aliquot of the sample solution was injected into the HPLC system.

The HPLC system consisted of same composition described in section 1.1. The column of Merck Lichrospher 100 RP-8 (e) 4×250mm was used for the analysis of vitamin K in mackerel and saury, and the Cosmosil 5C18-AR column 4.6×100mm (Nacalai Tesque, Inc. Kyoto, Japan) for marbled sole and sillago. A platinum oxide column, 4×20mm (EICOM Co., Kyoto Japan) was used as a reduction column. The mobile phase, flow rate and detection of vitamin K were same manner as section 1.1. The peaks were identified by comparison of retention times with those of the standards and disappearance of peaks without reduction.

Results

The body measurements of the fishes used for this study were shown in Table 3. The size of fish was not greatly different from each other in samples of the same species. Except for marbled sole, sillago and saury were not mature. The gonad of mackerel was too small to determine GSI.

The PK and MKs contents in the fish tissues were illustrated in Fig. 5. None of the samples showed even trace of MK-9. In mackerel, though MK-6 was detected, no other long chain Mks were detected. Similarly, in the case of sardine, the content of PK was much higher than those of MKs. This was especially so in the liver where the PK content was as high as 3-4 times when compared to those in heart and kidney. However, only a trace amount of vitamin K was detected in the ordinary and dark muscle tissues. Thus the vitamin K distribution pattern in mackerel was very similar to that of sardine, although the amount in the former was two times higher than that of the latter.

In striking contrast to mackerel, MK-4 appeared to be the major vitamin K in the heart and gonad of saury with very low level of PK. Furthermore, little vitamin K was present in the liver. The total vitamin K content was, however, much lower than that of mackerel.

In the case of marbled sole, significant amounts of long chain MKs (MK-6 and 7) were detected together with MK-4 in the heart and kidney. Furthermore, MK-8 was also found in the kidney. On the other hand, in sillago, PK and MK-4 were commonly distributed in the various organs, but MK-6, 7 and 8 were found only in the liver. In both marbled sole and sillago, the PK level was higher than that of saury on the whole but very much lower than that of mackerel.

As shown in Table 4, the contents of PK and MKs in the contents of gastrointestinal (GI) tract contents differed greatly among species. In the GI tract contents of marbled sole and sillago, large amounts of the long chain MKs were detected. However, in the mackerel and saury, the contents of long chain MKs was less than 1/100 of those of marbled sole and sillago. The GI tract content of mackerel was

Table 3. Body length, body weight, sampling locality and date of fish used for determination of vitamin K

	Body length(cm)	Body weight(g)	GSI[1]	Sampling locality	Sampling date
Mackerel	24.6±0.5	197±21	-[2]	Sagami Bay	2 Nov. 1993
Saury	29.0±0.6	156±14	0.20±0.17	East of Hokkaido	2 Nov. 1993
Marbled sole	16.7±0.4	113±9.0	4.07±2.59	Tokyo Bay	2 Nov. 1993
Sillago	15.0±0.5	44.1±4.5	0.62±0.20	Tokyo Bay	2 Nov. 1993

[1] Gonad somatic index (Gonad weight × 100 /Body weight).

[2] Not measured.

Values are means ± SEM of 5 fish.

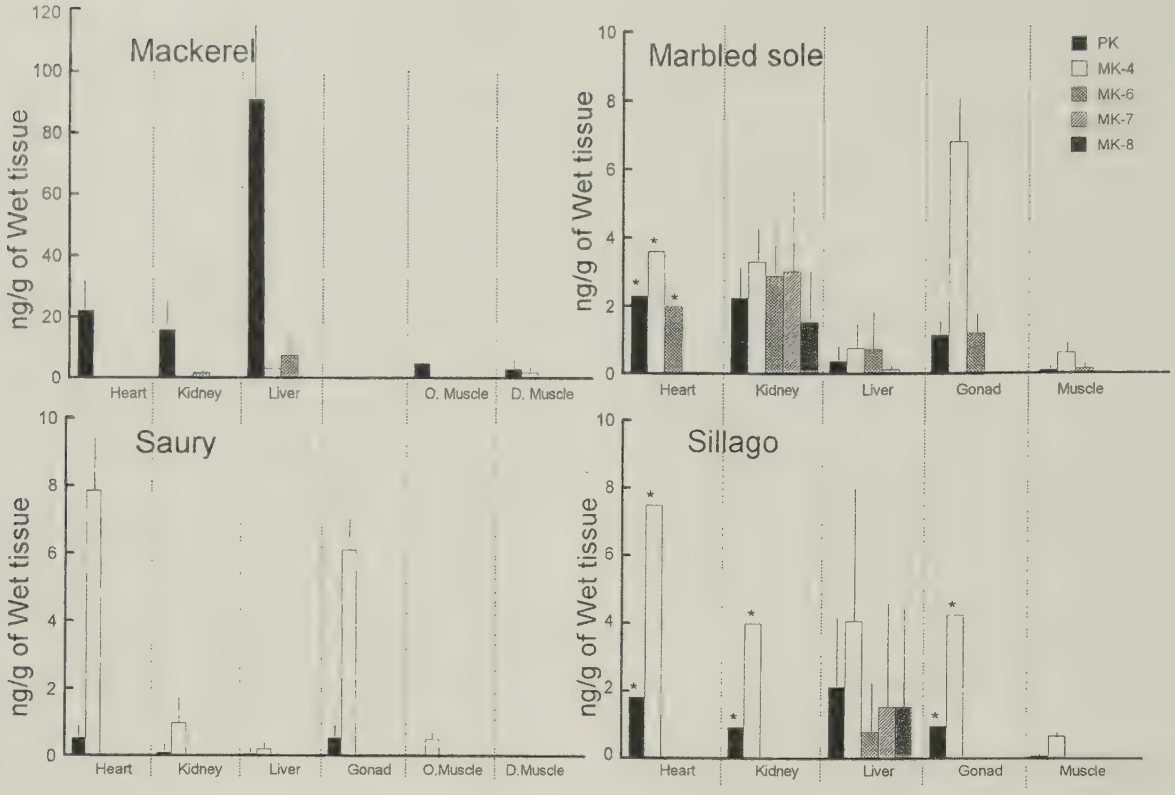


Fig. 5. Contents of phylloquinone (PK) and menaquinone (MK)-4, 6, 7, 8, 9 in various tissues of mackerel, saury, marbled sole and sillago. O muscle: Ordinary muscle, D muscle: Dark muscle. Values are means ± SEM of 5 fish. * Indicates that the values were measured by pooling specimens from 5 fish. MK-9 was also analyzed, but not detected in all the tissues examined.

Table 4. Contents of phylloquinone and menaquinone in gastrointestinal tract contents of fish
(ng/g of wet substance)

	PK (%)	MK-4 (%)	MK-6 (%)	MK-7 (%)	MK-8 (%)	MK-9 (%)
Mackerel						
Stomach	3.97±2.04(32)	1.29±0.26(10)	3.83±0.87(31)	3.28±2.31(27)	N.D.	N.D.
Intestine	2.01±0.98(34)	0.24±0.03 (4)	2.37±1.05(40)	1.07±0.24(18)	0.18±0.28 (3)	N.D.
Saury						
Stomach	0.74±0.65(10)	2.62±1.49(35)	2.11±2.04(28)	1.96±1.53(26)	N.D.	N.D.
Intestine	2.48±0.69(13)	5.79±1.03(29)	5.61±2.05(28)	5.98±4.23(30)	N.D.	N.D.
Marbled sole						
Stomach	54.8±50.8 (6)	20.3±15.1 (2)	228±343 (24)	408±582 (44)	160±143 (17)	62.7±67.0(7)
Intestine	12.6±11.7 (4)	4.76±2.72 (2)	95.1±164(30)	159±279 (49)	39.1±54.0(12)	13.7±23.8(4)
Sillago						
Stomach	9.82±11.8 (6)	6.34±3.66 (4)	67.5±103(43)	53.5±66.7(34)	14.6±14.6 (9)	3.98±5.97(3)
Intestine	19.9±21.9 (8)	10.0±5.37 (4)	75.1±89.0(28)	94.1±54.4(36)	47.2±48.4(18)	18.4±25.8(7)

N.D.:not detected.

Values means ±SEM of five fish.

(%):percentage of each vitamin K to total vitamin K volume

Table 5. Phylloquinone and menaquinone contents in food consumed by fish
(ng /g of wet substance)

	PK (%)	MK-4 (%)	MK-6 (%)	MK-7 (%)	MK-8 (%)	MK-9 (%)
Euphausia pacifica	0.35(6)	1.76(28)	2.63(41)	1.61(25)	N.D.	N.D.
Polychaeta spp.	11.6(4)	28.8(11)	48.9(18)	139 (51)	32.4(12)	14.2(5)

N.D.: not detected.

rich in PK, MK-6 and MK-7 and that of saury was rich in MK-4, 6 and 7. However, in the GI tract contents of marbled sole and sillago, MK-6 and 7 were the major components and the proportions of PK and MK-4 were very low. The composition of vitamin K was very similar between the stomach and intestinal contents of the same species of fish.

The PK and MK contents in food organisms are shown in Table 5. In *Euphausia pacifica*, the PK and MK levels were low, and its composition of vitamin K was similar to those of the GI tract contents of mackerel and saury with an exception of the low PK. On the other hand, in *Polychaeta spp.* MK-7 was the major vitamin K followed by MK-6 and MK-8, with a trace or negligible amount of PK. This composition resembled those of the GI tract contents of marbled sole and sillago. From these results it can be concluded that the compositions of vitamin K in food organisms and that of GI tract contents are similar to each other.

Discussion

Mackerel and saury feed on plankton, small fish and copepoda (Usami, 1968). The vitamin K composition of the GI tract contents of saury was similar to that of, Pacific krill *Euphausia pacifica*, suggesting that vitamin K in the GI tract of saury came from their food. While in mackerel, the vitamin K composition of GI tract seems to be different from that of *Euphausia pacifica*. However, it can be regarded that significant difference in vitamin K composition is only PK between content of the GI tract and that of *Euphausia pacifica*, so that there may be another supplementary source for PK in the case of mackerel. On the other hand, marbled sole and sillago feed on benthos such as *Polychaeta spp.* (Maeda 1955; Maeda 1955; Omori 1974). The composition of vitamin K of the GI tract contents of these specimen were similar to that of *Polychaeta spp.* This also suggests that the vitamin K in the GI tract contents depends on their food. Therefore, it is possible that the vitamin K in the tissue of the fishes studied originated from their GI tract, because all forms of vitamin K present in GI tract were also detected in the tissue of a certain organ, though a slight difference was detected between the vitamin K composition of stomach and that of intestinal contents. It implies that fish cannot produce long chain MKs in the intestine on its own.

In the GI tract contents, MK-7 was one of the major vitamin K components in mackerel and sillago, however there was little MK-7 in the other tissues of these fishes. In the cases of mackerel and saury, their GI tract contents were rich in long chain MKs, but, in the tissue, only a little long chain Mks were detected. This suggests that all of vitamin K in the food was not transferred into the tissues of fish and there must be a selected absorption mechanism. It is known that MK-4 is conversion from PK at chick and rat tissues (Thijssen and Drittij-reijnders 1994; Will *et. al.* 1992). It is possible that Mk-4 in these fish tissues comes from PK which depends on their food.

In the liver of mackerel, the PK contents was outstanding. There was, however, not such a high level in the tissue of other fishes examined. There must be a possibility that vitamin K in different forms might be selectively absorbed and deposited in the tissue. Furthermore, the selection and degree of deposition may differ among the species of fish and/or different organs. Though the contents of

long chain MKs in the tissue of fish were not so high as those in the GI tract, it is characteristic of the kidney and liver to contain various forms of long chain MKs. These data suggest that vitamin K in fish was used in various forms, but the absorption rates may differ in the form of vitamin K.

1.2.2. Comparison of the composition of vitamin K in different forms between cultured and wild fish

Long chain MKs such as MK-7 and MK-9 are major forms of the utilizable vitamin K in mammals (Usui *et al.* 1989), but for fish the major utilizable forms are PK and MK-4. However, the utilizable form of vitamin K differs with feeding habits and fish species. In this section, ayu *Plecoglossus altivelis* was studied because it is an abundant, economically import and valuable freshwater fish. Wild ayu inhabit rivers and feed on diatoms. Ayu is also extensively cultured in Japan. The contents of PK and long chain MKs in the tissues were measured and the tissue distribution pattern between the wild and cultured fish was compared.

Materials and Methods

Wild ayu caught in the Chikuma river in Nagano Prefecture on 15 September 1993 were used for this study (body length: 17.5cm; body weight: 69.5g). Ayu at the larvae stage caught at Biwa Lake in Siga Prefecture were reared in an outdoor tank at the Ueda Station of National Research Institute of Fisheries Science in Nagano Prefecture, were used as the cultured fish sample. They were fed with a commercial diet containing MSB for 5 months. They were 14.5cm in length and 45.0g in weight. All of the fish were frozen-stored at −40℃ until use. Diatoms were collected from the surfaces of stones at the bottom of river where the wild ayu were caught. The PK and MKs contents were measured by the HPLC method in the same manner as section 1.2.1. MSB was analyzed according to the same method as section 1.1.1.

Result and Discussion

The PK and MKs contents in various tissues are illustrated in Fig. 6. In the tissues of wild ayu, PK appeared to be the major form of vitamin K, and MKs was present at very low levels. Long chain

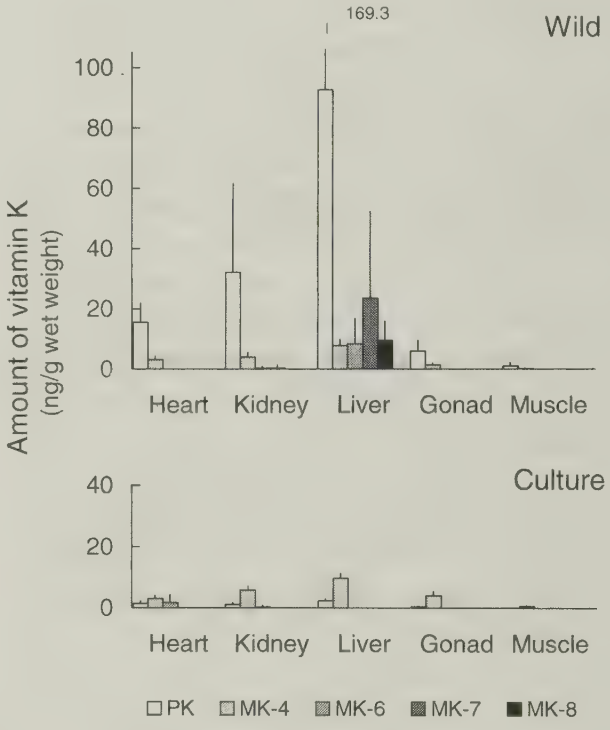


Fig. 6. Amount of phylloquinone and menaquinones in different tissues of wild and cultured ayu. Values are means ± SEM of five fish (cultured fish) and ten fish (wild fish). MK-9 was not detected in all tissues examined.

Table 6. Phylloquinone and menaquinones contents in feed consumed by ayu (ng/g)

	PK	MK-4	MK-6	MK-7	MK-8	MK-9	MSB
Diatom	164 (38)	31.8 (7)	30.8 (7)	137 (32)	71.5 (16)	-	
Commercial diet	38.6	10.2	-	-	-	-	1.2×10^3

MSB=menadion sodium bisulfite (Figures in parentheses are expressed as percentage.)

Table 7. Amount of different forms of vitamin K in the stomach and intestine of wild and cultured ayu

(ng/g wet weight)

	PK	MK-4	MK-6	MK-7	MK-8	MK-9
Wild						
Stomach(0.22)*	107.7 (62.1)	8.2 (4.7)	4.8 (2.8)	32.7 (18.9)	20.1 (11.6)	-
Intestine(0.34)*	440.9 (79.3)	6.9 (1.2)	8.6 (1.6)	74.9 (13.5)	24.3 (4.4)	-
Cultured						
Stomach(0.24)*	80.1 (30.6)	24.7 (9.5)	98.7 (37.7)	51.8 (19.8)	6.4 (2.4)	-
Intestine(0.37)*	22.6 (9.5)	5.8 (2.4)	120.8 (50.8)	65.5 (27.5)	23.2 (9.8)	-

(Figures in parentheses are expressed as percentage of total vitamin K in each specimen.)
*= weight/body weight (percentage).

MKs in the different forms were present in the liver, but their quantities were lesser than that of PK. Only MK-6 was detected in tissues other than the liver. On the other hand, in the tissues of cultured ayu, the major form of vitamin K was MK-4, while MK-6 was detected only in the heart and kidney. Unlike the wild ayu, no long chain MKs were observed in the liver.

The PK and MKs contents in the feed given to ayu are shown in Table 6. PK is abundant in diatoms. In the gastrointestinal (GI) tract content of wild ayu fed with diatoms, the PK content accounted for 60-80% of total vitamin K (Table 7). It is, therefore, certain that the PK in the GI tract originated from diatoms in the diet. As for cultured ayu, long chain MKs was the major form of vitamin K in the GI tract. However, MSB could not be detected in the GI tract. This is because MSB which was added to commercial feed, a water soluble form, cannot be detected by this HPLC method. It was reported that the alkylation of MD to MK-4 in the liver differs between chick and rat liver (Dialameh *et al.* 1970, 1971). In the ayu, this conversion process is thought to be active resulting in high levels of MK-4 in the tissues.

In each group of fish, large quantities of long chain MKs, which were considered to be of bacterial origin, were detected in the contents of GI tract (Table 7). However, only small amounts were found in the tissues (Fig. 6). This suggests negligible absorption of long chain MKs into the tissues of the fish. Further studies are required to prove the existence of MK-producing bacteria in the GI tract and the low utilization of their by-products. From this observation, it is probable that MK-producing bacteria could not be a major source of vitamin K in the ayu. These findings also suggest that the extent of absorption and/or conversion of vitamin K in the tissues of the ayu varies with the different forms of vitamin K.

In the liver, most of the vitamin K present was in the form of PK in the wild ayu and MK-4 in the cultured ayu (Fig. 6). The quantity of PK in the wild ayu was about 10 times higher than that of MK-4 in the cultured ayu. This observation is similar to those results for sardine and mackerel. The reason why PK is accumulated at a much higher concentration as compared with MK-4 has yet to be elucidated. However, since evidence has been reported that mice and chickens have the ability to convert PK into MK-4 (Thijssen and Drittij-Rejinders 1994; Thijssen *et al.* 1996; Will *et al.* 1992), the fact, the much higher concentration of PK and low concentration of MK-4 in wild ayu, may be attributed to the weak conversion ability in ayu.

Chapter 2. Absorption of vitamin K in fish

The dietary necessity and physiological roles of vitamin K are fairly well established for mammals (Dan 1935) and its importance in bone health has been recently a focus for research (Vermeer *et al.* 1996). However, it is still not clear whether dietary supplementation of this vitamin is indispensable for the growth of fish because of contradictory results have been reported between fish species (Poston

1964; Kitamura *et al.* 1967; Murai and Andrews 1977; Taveekijakarn *et al.* 1996).

PK, MK and MD are known to be converted partly into MK-4 in the tissues of calves (Nestor and Conrad 1990). Similarly, PK has been shown to be converted into MK-4 in mice and chickens (Will *et al.* 1992), and MD into MK-4 in cod (Grahl-madsen and Lie 1997). The distribution pattern of vitamin K in the tissues of fish has been reported to differ with the feeding habit among fish species and the PK content is usually much higher than MK in wild fish. The PK content in the gastrointestinal tract is high, then always high PK level is detected in the liver, while even though relatively large amounts of MKs are found in the gastrointestinal level, not all forms of MKs are detected in fish. However, the mechanism and rate of absorption of the various vitamin K groups have not been clarified yet in fishes.

This chapter describes the concentrations of the vitamin K derivatives in the tissues of males and females mummichog after feeding diets supplemented with different forms of vitamin K as a first step to elucidate the physiological role of vitamin K in fish.

Materials and Methods

Mummichog *Fundulus heteroclitus* were fed a

Table 8. Composition of the experimental diet

	Diet						
Experimental group	No. 1 Group 1	No. 2 Group 2	No. 3 Group 3	No. 4 Group 4	No. 5 Group 5	No. 6 Group 6	No. 7 Group 7
Ingredient (g / 100g)							
Vitamin-free casein*[1]	30	30	30	30	30	30	30
Gelatin*[2]	5	5	5	5	5	5	5
Dextrin	30	30	30	30	30	30	30
Feed oil*[3]	8	8	8	8	8	8	8
Mineral mix*[4]	4	4	4	4	4	4	4
Vitamin mix*[5]	4	4	4	4	4	4	4
Calcium lactate	0.08	0.08	0.08	0.08	0.08	0.08	0.08
Sodium phosphate, monobasic	0.48	0.48	0.48	0.48	0.48	0.48	0.48
CMC*[6]	5	5	5	5	5	5	5
Cellulose	13.44	13.44	13.44	13.44	13.44	13.44	13.44
Vitamin K (mg / kg)							
Phylloquinone	-	1	-	-	-	-	-
Menaquinone-4	-	-	1	-	-	-	-
Menaquinone-6	-	-	-	1	-	-	-
Menaquinone-7	-	-	-	-	1	-	-
Menaquinone-8	-	-	-	-	-	1	-
Menaquinone-9	-	-	-	-	-	-	1

*[1]: (Lot no. ECF7046) Wako Pure Chemical Industries (Osaka, Japan).

*[2]: DIFCO Laboratories (Detroit, USA).

*[3]: (Lot no. SNo. J-450) Riken Vitamin Company, Ltd. (Tokyo, Japan).

*[4]: Mc.Collum Salt 820517 Iwai Chemical Co., Ltd. (Tokyo, Japan).

*[5]: The premix reported by the National Research Council was partly modified as follows (mg / 4 g premix): thiamin HCl 5, riboflavin 20, pyridoxine HCl 5, choline chloride 500, nicotinic acid 75, ca-pantothenate 50, inositol 200, biotin 0.5, folic acid 1.5, ascorbic acid 100, alpha-tocopherol 40, vitamin B_{12} 0.01, activated 7-dehydro-cholesterol 200IU, retinol 3200IU.

*[6]: Carboxymethylcellulose-Na.

commercial diet for common carp in an outdoor tank of 4.5m^3 (sea water depth: 1.5m). All the experimental fish were acclimated to the experimental conditions described below by feeding the vitamin K deficient diet for three weeks prior to the start of the experiment. The experimental fish (average body weight of 18.1g) were divided into seven groups of 3 pairs each. Each group was transferred to respective 20L glass aquariums placed in the laboratory and supplied with running natural seawater. The experimental fish were reared in a 3mm mesh screen cage placed in the aquarium so that they were unable to eat their own feces and eggs. The water temperature was kept at 20℃ and the laboratory was lit with fluorescent lights for 13 hours from 7: 00 throughout the experimental period.

The basal diet was designed according to Murai *et al.* (1984). Fish in each group were fed an experimental diet respectively supplemented with different vitamin K derivatives (Table 8). No. 1: a vitamin K deficient diet; Nos. 2 to 7: supplemented with PK, MK-4, -6, -7, -8 and -9 at a ratio of 1mg/kg, respectively. Experimental diets were given at 2% of the body weight per day for 12 days.

Approximately 3 hours after the final feeding, samples of blood, kidney, liver, gonad and gastrointestinal tract were collected from individual fish to analyze the content of vitamin K derivatives in each specimen.

The PK and MKs contents were measured by the HPLC method in the same manner as section 1.2.1.

Results

The contents of PK and MKs in the gastrointesti-

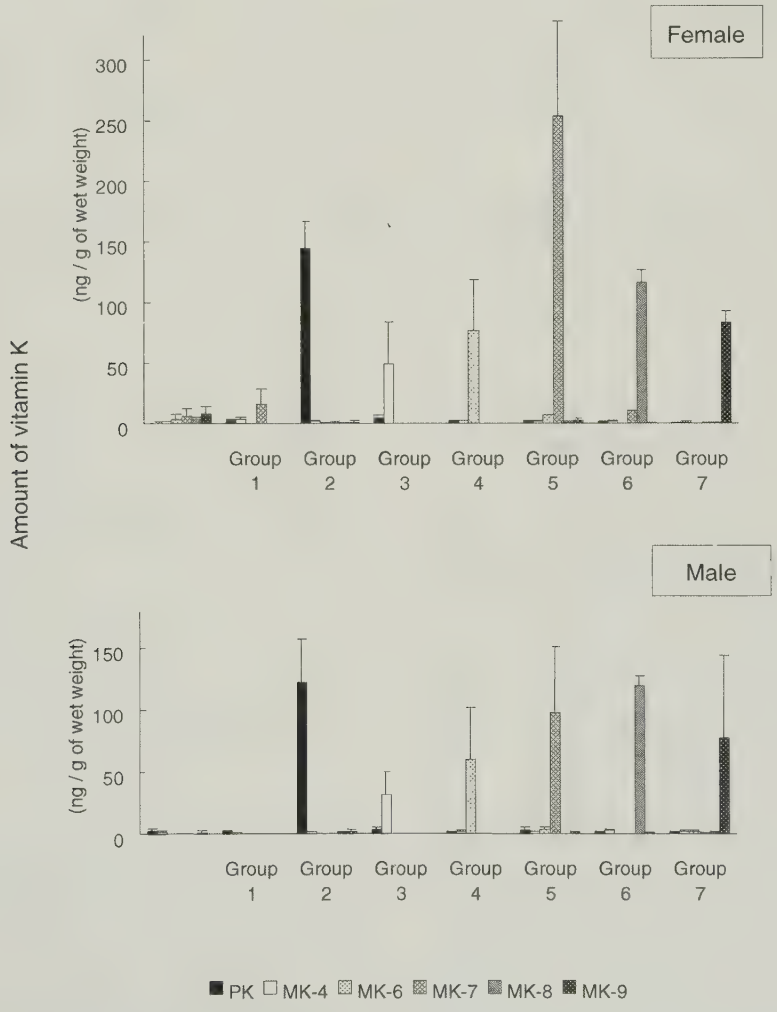


Fig. 7. Phylloquinone and menaquinone contents in the gastrointestinal tract contents of the each group of fish. Values are means ± SEM of 3 fish.

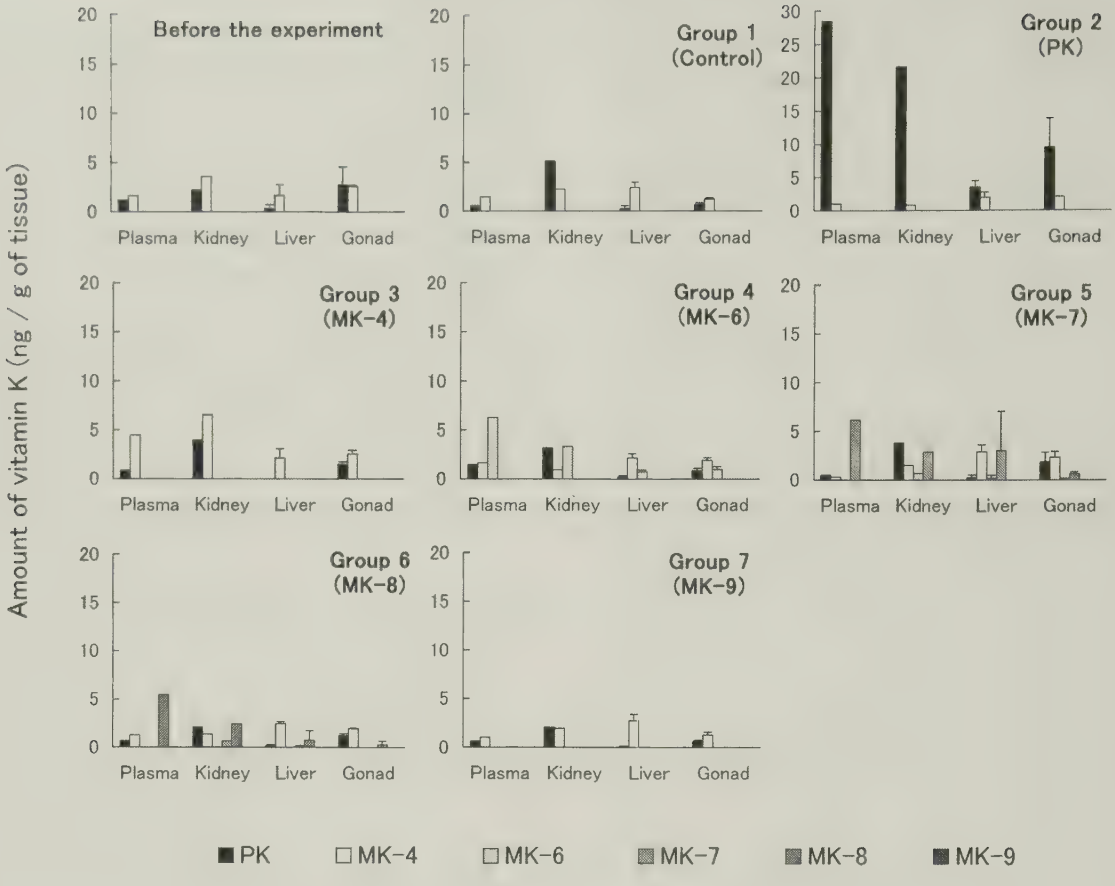


Fig. 8. Phylloquinone and menaquinone contents in four different tissues of female mummichog of each group of fish. Control fish (no vitamin K added) and each vitamin K added to the experimental diet. Values are means ± SEM of 3 fish.

nal tract are shown in Fig. 7, which were collected at about 3 hours after the final feeding of the respective diets. The contents of the various vitamin K derivatives reflected almost exclusively the dietary supplements even though there were some difference in their levels. These levels were somewhat higher in females than in males, especially for Group 5. Also, a small but significant quantity of MK-7 was detected in the females only of Group 1 although both females and males of this group were fed the vitamin K free diet for 33 days including the acclimatization period.

The concentrations of PK and MKs in the plasma, kidney, liver and gonad are shown in Fig. 8 for females and Fig. 9 for males. In both females and males, feeding of the vitamin K free diet for an additional 12 days (control group) made no change in the concentrations of vitamin K in the plasma and tissues which consisted only of PK and MK-4. The plasma levels of the various vitamin K derivatives which are a certain indication of absorption from the intestine, differed among the vitamin K fed, and between females and males. The plasma level of PK in Group 2 fed the PK supplemented diet was 30ng/ml in females but only about 1/3 of that value in males. Values of the MK derivatives were much lower than the PK value not only in males but also in females. On the whole, the values for females were much higher than the corresponding values for males. MK-9 having the longest side chain was not detected at all in the plasma.

PK was accumulated in the kidney, liver and gonad of fish fed the PK-supplemented diet in both females and males. Reflecting the plasma level, the PK concentration in the kidney of females was much higher than males, but this was not true for the liver and gonad. In case of males, contents of MK-4 in the liver were highest even in the groups fed the other

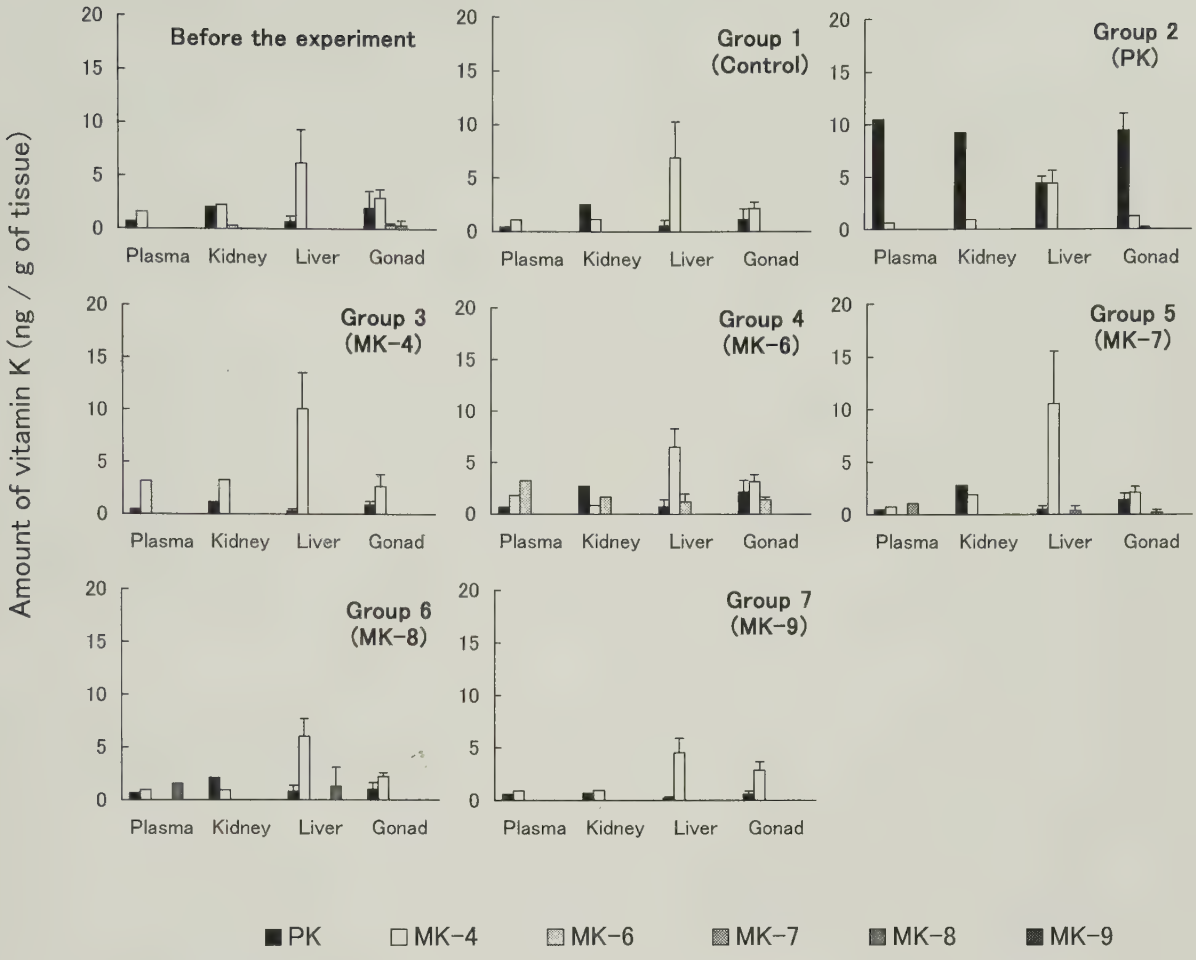


Fig. 9. Phylloquinone and menaquinone contents in four different tissues of male mummichog of each group of fish. Control fish (no vitamin K added) and each vitamin K added to the experimental diet. Values are means ± SEM of 3 fish.

derivatives. While, MK-6, MK-7, and MK-8 were more clearly detected in the tissues of females than in males. However, MK-9 was not detected at all in any tissues examined.

PK and MKs which were not supplemented in the diet were detected in the tissues of almost every dietary groups at similar levels as prior to the experiment and of the control group (Group 1).

Discussion

As shown in Fig. 7, the major vitamin K in the gastrointestinal tracts of each experimental group was that administered in the feed to the respective group and only minute amounts of the other homologues were recognized in each group. This clearly indicates that the major vitamin K source is almost entirely of dietary origin.

The fish were found to contain very small amounts of PK and MK-4 in the plasma at the beginning of the experiment. Because the experimental fish were fed a commercial diet with MSB until the start of feeding the experimental diets, the small amount of MK-4 detected in all groups should be taken into account. The plasma levels of vitamin K derivatives shown Figs. 8 and 9 imply that PK is the most efficiently absorbed into the blood in both females and males because its level was much higher than those of the MK derivatives. This result agrees well with Birgit and Suttie (1992) who reported that the PK level in the plasma of rats fed a PK-supplemented feed was about three times higher than rats fed a MK-9 supplemented feed. Ichihashi *et al.* (1992) described that the absorption

rates of MKs decrease markedly with an increase in the number of isoprenoid units in rats. Akiyama *et al.* pointed out that the number of isoprene units of MK is an important factor in its absorption and incorporation into the liver in rats (1995). No clear relationship between the number of isoprene units and absorption was detected in this study. However, the side chain of MK-9 may be too long for mummichog to absorb it into the blood, because MK-9 was not detected at all in the plasma of both females and males.

As to the difference in the effectiveness in vitamin K activity, Groenen-van Dooren *et al.* observed that MK-9 was definitely more active than PK and MK-4 in rats (1995). While Thijssen reported that MK-4 rather than PK may be the functional vitamin in rats (1996). From the viewpoint of the effective accumulation of vitamin K in the tissues, PK can be considered to be a more available vitamin K in fish than any of the MK homologues and MD, differing from the case of rats. This view may be supported by the fact that the major vitamin K detected in the body of fish is generally PK. Therefore, further studies on the differences in the mechanism of absorption of PK and MKs are needed with respect to the supplementation of commercial feed for fish culture with vitamin K.

Judging from the vitamin K derivatives in the tissues, PK and MK-4 may play a major role in males as has been described at Chapter 1 in wild fishes. However, not only PK but also other MKs except MK-9 may play a certain important role in females. There were also apparent differences in the absorption of PK and MK-4, and in the accumulation of MKs in the tissues, especially MK-4 in the liver between females and males.

Chapter 3. Physiological function of vitamin K in fish

Vitamin K is well known for its participation in blood coagulation. Further, a variety of vitamin K deficiency diseases have been reported for mammals. In particular, human infants of a few weeks old are said to be exposed to a risk of hemorrhage due to vitamin K deficiency (Greason and Kerr 1989). Recently, the importance of vitamin K to bone health has also been emphasized (Vermeer *et al.* 1996).

There are some reports on vitamin K requirements for fish. As for rainbow trout and catfish, no perceivable syndrome of vitamin K deficiency was observed (Kitamura *et al.* 1967; Murai and Andrews 1977). On the other hand, Taveekijakarn *et al.* (1996) reported that mortality in vitamin K deficient fish, amago salmon, reached to about 50%.

From these researches on the role of vitamin K in fish it is difficult to conclude categorically whether vitamin K is essential for fish. In this chapter, experiment was undertaken to determine the vitamin K requirements of fish and to examine if there is any change in the distribution and/or the content of vitamin K in the organs, including eggs of fish fed with a vitamin K deficient diet for a long term spawning stage.

3.1. Physiological abnormality and the tissue vitamin K level in the fish fed with a vitamin K free diet

Mummichog *Fundulus heteroclitus* which is widely distributed along the eastern coast of North America, were chosen as the experimental fish, as this species is relatively easy to rear and the spawning season is long lasting. This section describes the experimental results of the change in vitamin K content in different organs of fish fed with a vitamin K supplemented or deficient diet for 11 weeks. Microscopic observations on the tissues of the fish are also described.

Since MSB, which has been proven to be converted into MK-4 after intake, is generally supplemented in the commercial diet of cultured fish, MSB was used for a control diet in this study.

Materials and Methods

Experimental fish and diet

Mummichog were fed a commercial diet in an outdoor-tank of 4.5m^3 (sea water depth: 1.5m). All fish were acclimated to the experimental conditions as follows for three weeks. The experimental fish were divided into three groups of 18 pairs each. Each group was transferred to respective 60L glass aquariums filled with running natural sea water

Table 9. Percentage composition of experimental diet

Ingredient	Diet		
	No. 1	No. 2	No. 3
Vitamin-free casein*[1]	30	30	30
Gelatin*[2]	5	5	5
Dextrin	30	30	30
Feed oil*[3]	8	8	8
Mineral mix*[4]	4	4	4
Vitamin mix*[5]	4	4	4
Calcium lactate	0.08	0.08	0.08
Sodium phosphate, monobasic	0.48	0.48	0.48
CMC*[6]	5	5	5
Cellulose	13.44	13.44	13.44
MSB*[7]	0.0025	0	0
Sulfaguanidine	0	0	0.1

*[1]: (Lot no. ECF7046) Wako Pure Chemical Industries (Osaka, Japan).
*[2]: DIFCO Laboratories (Detroit, USA).
*[3]: (Lot no. SNo.J-450) Riken Vitamin Company, Ltd. (Tokyo, Japan).
*[4]: Mc.Collum Salt 820517 Iwai Chemical Co., Ltd. (Tokyo, Japan).
*[5]: The premix reported by National Research Council was partly modified as follows (mg / 4.5 g premix): thiamin HCl 5, riboflavin 20, pyridoxine HCl 5, choline chloride 500, nicotinic acid 75, ca-pantothenate 50, inositol 200, biotin 0.5, folic acid 1.5, ascorbic acid 100, alpha-tocopherol 40, vitamin B_{12} 0.01, activated 7-dehydro-cholesterol 200IU, retinol 3200IU.
*[6]: Carboxymethylcellulose-Na.
*[7]: Menadione sodium bisulfite.

in the laboratory. The fish in respective groups were referred to as Groups 1, 2 and 3. The basic diet was designed according to Murai *et al.* (1984). The composition of the diet is given in Table 9. Group 1 was fed with the control diet (No. 1) which was supplemented with MSB. Group 2 was fed with the vitamin K free diet (No. 2). Group 3 was given another vitamin K free diet (No. 3) to which sulfaguanidine (SG) was added to eliminate the possibility of any effect of vitamin K production by intestinal bacteria. All of the fish were fed five times a day on 2.5% of body weight with an automatic feeder for 11 weeks. The fish were kept at 22℃ with 14 h of light per day (6:00 to 20:00). Experimental fish were reared in a 3-mm mesh screen cage placed in the aquarium so that they did not eat their own feces and eggs. The inner wall of each aquarium was carefully cleaned three times a week. On all such occasions, fish were transferred within the screen cage to another aquarium, and naturally spawned fertilized eggs that sank through the screen to the aquarium bottom were collected once a week with a fine mesh net. The experiment started on June 6, 1995. After 11 weeks of feeding, five fish from each group were killed to measure the vitamin K levels in the heart, kidney, gonad, liver, muscle, gill and plasma, and for another five fish kidneys, livers, spleens were histologically examined. The eggs were transferred in a fine net to a separate tank (area: 60×40cm, depth: 10cm) with running sea water. Larvae (about 200) were fed with the same diet as that given to their parent fish beginning immediately after hatching. They were reared in a 5L aquarium with running natural sea water. The mortality of experimental fish after 4 weeks of feeding was examined. Triplicated

Table 10. Effect of dietary MSB on the growth, condition factor and mortality of mummichog

Group	Sex	Body weight (g) Initial*2	Body weight (g) 11 weeks	Length (mm) 11 weeks	Condition factor	Growth*1 rate (%)	Mortality (%)
1	female	11.47	13.28[a]	81.41[ab]	2.44[a]	1.16[a]	16[a]
	male	11.47	10.94[b]	78.81[b]	2.21[b]	0.95[b]	11[a]
2	female	10.50	11.51[ab]	77.94[b]	2.44[a]	1.10[a]	16[a]
	male	10.50	-	-	-	-	100[b]
3	female	11.47	13.25[a]	83.72[a]	2.23[ab]	1.16[a]	26[a]
	male	11.47	-	-	-	-	94[b]

Values in the same column with different superscripts are significantly different ($p<0.05$).
*1: body weight (11 weeks) / Initial body weight.
*2: The fish were pooled and weighed.

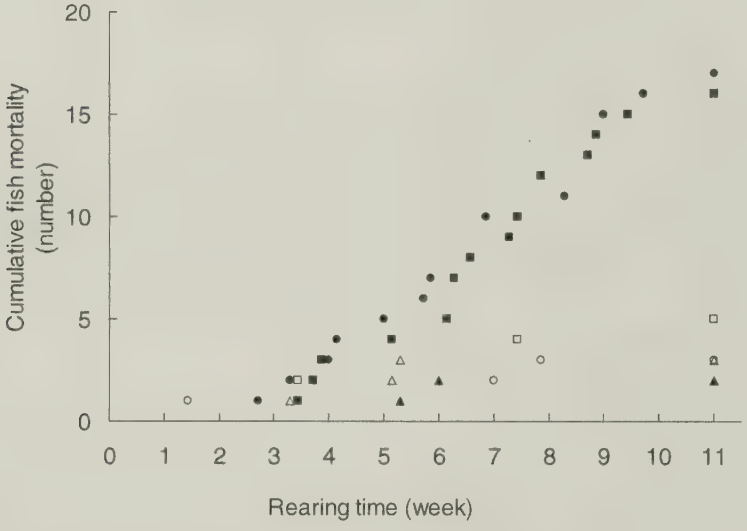


Fig. 10. Cumulative fish mortality of the three groups.
Open and solid symbols represent female and male fish, respectively. Triangle (△, ▲), control fish fed with the No. 1 diet which was supplemented with MSB; Circle (○, ●), experimental fish fed with No. 2 diet which is MSB free; Square (□, ■), experimental fish fed with No. 3 diet which is MSB free containing sulfaguanidine.

sampling was carried out on eggs and larvae to examine the hatching rate and mortality of the larvae.

Vitamin K Analysis

PK and MK were measured by the same method described in Section 1.2.1. In the case of spawned egg and larvae specimens, 100 individuals of each were pooled and homogenized.

Histological Observations

The kidney, liver and spleen excised from the experimental fish were fixed with Bouin's fluid and embedded in paraffin. Serial sections 5 μm thick were stained with hematoxylin and eosin.

Statistical Analysis

Data for the gonads of female fish at the beginning of the experiment and those in Group 1 were analyzed by the Wilcoxon rank sum test, the other

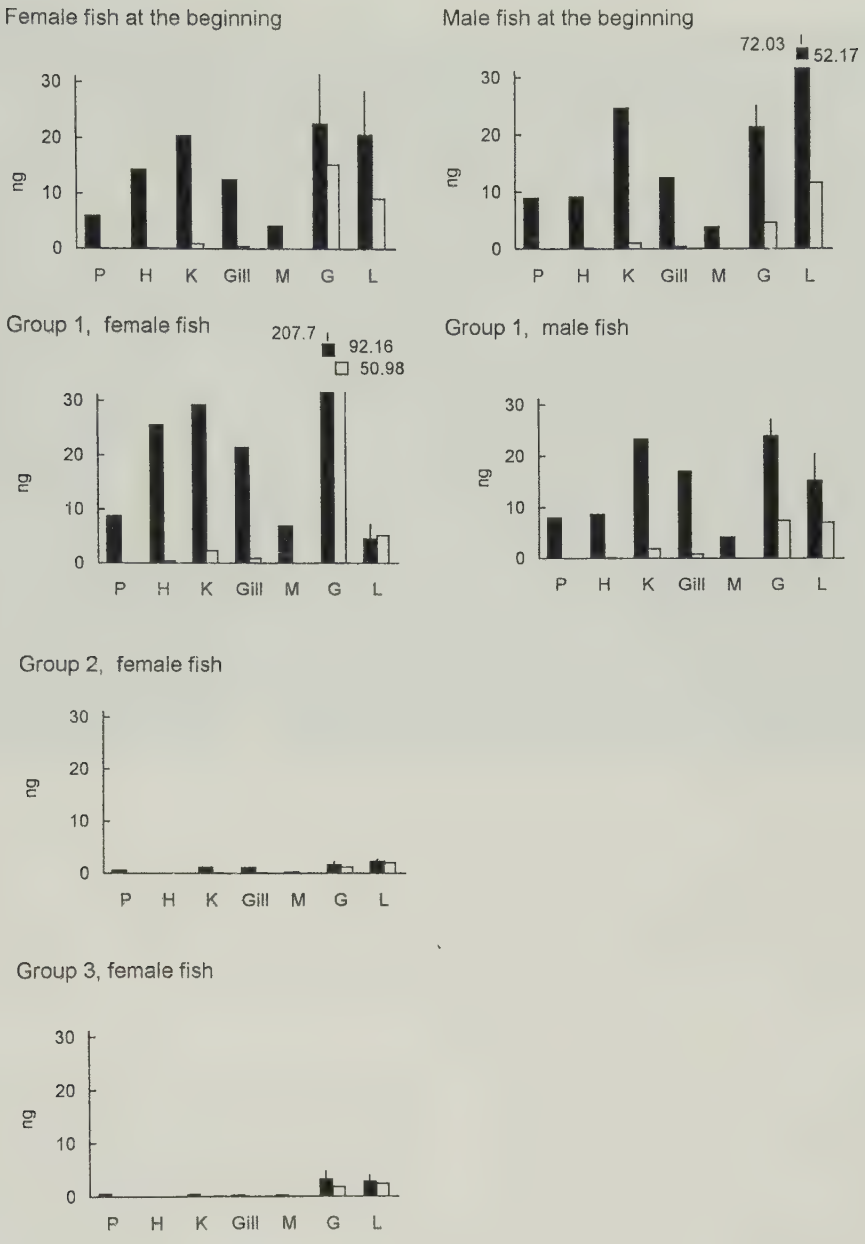


Fig. 11. Menaquinone-4 (MK-4) contents in various tissues of mummichog.
P, plasma; H, heart; K, kidney; M, muscle; G, gonad; L, liver. Values for the gonad and liver are means ± SEM of 5 individuals. Other tissues were measured using pooled samples of the 5 fish. Solid column, ng per g of tissue; open column, ng per whole body.

data by Duncan's multiple range, multiple *F*-test (Duncan 1955).

Results

There was a striking contrast in mortality between the control (Group 1) and experimental fish (Groups 2 and 3) as shown in Table 10. In Groups 2 and 3, most male fish died. There was no such great difference in the female fish mortality. No significant difference was observed in the growth rate of female fish among the 3 groups. Figure 10 shows the cumulative number of fish that died during the experimental period. In Group 2, the first male fish died on day 20, and by the 11th week all the male fish had died. For the fish fed with the

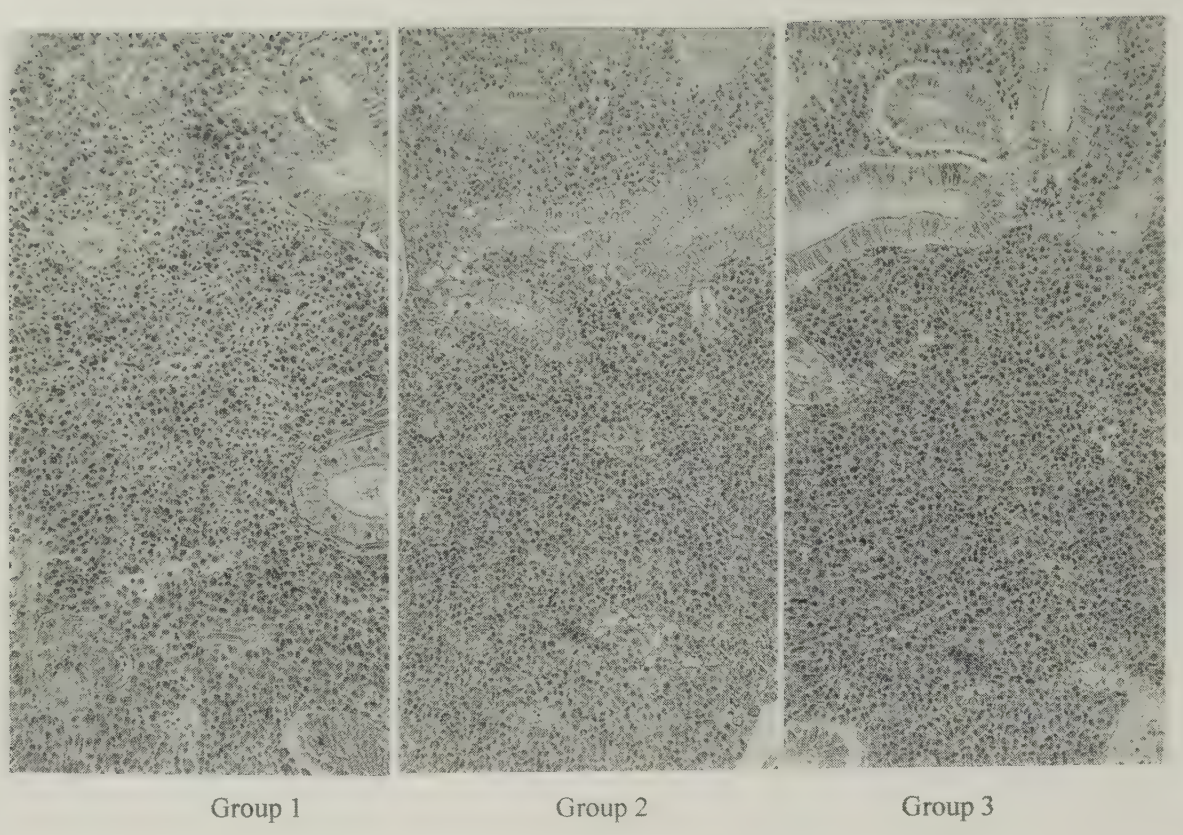


Fig. 12. Effects of vitamin K deficient diets on the kidney of a female mummichog (hematoxylin and eosin), showing a large number of erythrocytes including immature cells.
Group 1, fed with control diet; Group 2, fed with vitamin K deficient diet; Group 3, fed with vitamin K deficient diet supplemented with sulfaguanidine. Magnification: ×66.

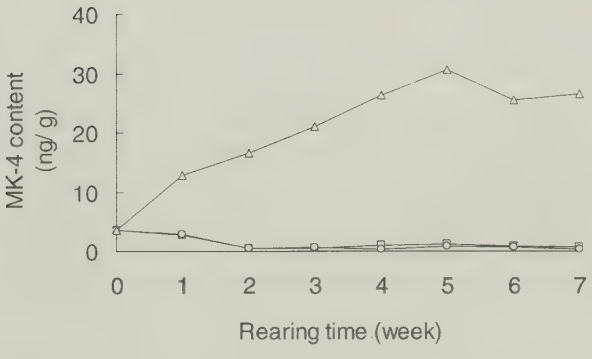


Fig. 13. Changes in menaquinone-4 (MK-4) contents in the eggs.
Triangle (△), egg spawned by the fish fed with a MSB supplemented diet; circle (○), eggs spawned by the fish fed with vitamin K free diet; square (□), eggs spawned by the fish fed with a sulfaguanidine supplemented diet. All eggs were pooled for analysis.

No. 3 feed (Group 3), male fish also died frequently as in the case of fish fed with the No. 2 feed (Group 2), and only one male survived after the 11 weeks of experimental feeding with the vitamin K free diet. However, in the case of female fish, there was no significant difference in the mortality between the control (Group 1) and the experimental fish (Groups 2 and 3).

The MK-4 content in various tissues of the fish at the beginning of the experiment and for female fish after 11 weeks of feeding are summarized in Fig. 11. The MK-4 contents were markedly higher in the gonad and liver of the fish at the beginning of the experiment. In Group 1, the MK-4 content increased to some extent in most parts of the body, and markedly in the gonad, within the 11 weeks of feeding. However, in the liver, the content decreased significantly. The MK-4 content in the fish in Group 2 or 3 decreased to about one tenth

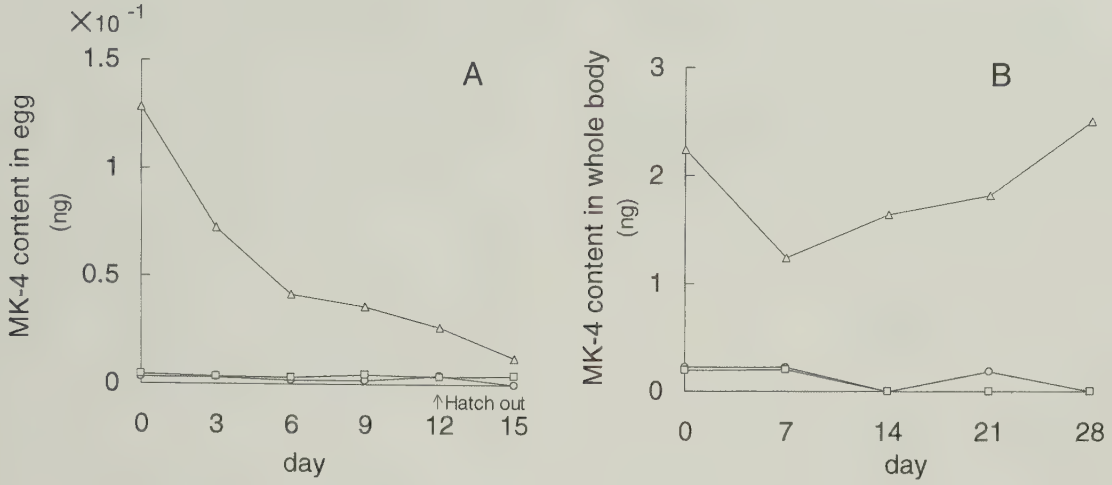


Fig. 14. A: Changes in the content of menaquinone-4 (MK-4) in the eggs of the three groups of fish during development. B: Changes in the content of MK-4 in the larvae from the three groups of fish.
The larvae were fed with the same feed as that for their parents. Triangle (△), egg or larvae from the fish fed with a MSB supplemented diet (No. 1); circle (○), egg or larvae from the fish fed with a vitamin K free diet (No. 2); square (□), egg or larvae from the fish fed with a sulfaguanidine supplemented diet (No. 3)

Table 11. Hatching rate and mortality of the three groups of mummichog larvae*

Diet	No.1	No.2	No.3
Hatching rate	59.7%	61.1%	72.2%
Mortality	27.8%	30.3%	20.6%

*All figures are the average value of triplicate experiments.

or less of the initial level. There was, however, no essential difference in the levels between these two groups of fish. Analysis of MK-4 for male fish in Groups 2 and 3 was not possible, because almost all of the male fish has died during the 11 week experiment. The reason for the extremely high content in the liver of the male fish at the beginning of the experiment can not be presently explained. PK was not detectable in every tissue.

According to microscopic observation of the tissues, abnormality was observed only in the kidney of fish in Groups 2 and 3 fed with the vitamin K free diets. A number of erythroblasts existed in the kidney of the fish in Groups 2 and 3. Particularly, many more erythroblasts were observed in Group 3 fish (Fig. 12).

The effect of vitamin K deficiency of the mother fish on the eggs and larvae, i.e. the hatching rate and the mortality of larvae, was investigated. Firstly, the relationship between egg MK-4 content and the duration of feeding of the mother fish fed with the experimental diet (No. 2 or No. 3) is shown in Fig. 13. The MK-4 content in eggs produced by the experimental fish (Groups 2 and 3) decreased to almost zero within the first 2 weeks, while the content in the eggs of Group 1 (control fish) rose steadily from the beginning of feeding, and reached a maximum level after 5 weeks.

Secondly, using eggs collected between the 6th and 7th week in the feeding experiment, the effects of MK-4 content of the eggs on the hatching rate and mortality of the larvae were examined. The content change of MK-4 in eggs and larvae are shown in Fig. 14 and B, respectively. MK-4 contents in both eggs and larvae from Groups 2 and 3 were very low throughout the egg development period and subsequent feeding period, respectively. On the other hand, MK-4 content in eggs spawned by

Group 1 fish decreased markedly from the beginning of development (Fig. 14). As for the larvae of Group 1 fish, the content became high after the first feeding (Fig. 14). However, there was no significant difference in the hatching rate and mortality of larvae among the three experimental groups (Table 11).

Discussion

The MK-4 content in fish fed with a vitamin K free diet decreased markedly during the 11 weeks of feeding (Fig. 11). This indicates that MK-4 in the control fish (Group 1) is derived from MSB in their feed. There was no significant difference in the MK content or mortality between the experimental group of fish fed with the SG added diet and the non SG diet, indicating that MK-long chain, if produced by intestinal bacteria in the fish in Group 2, does not influence the tissue levels of vitamin K.

In Group 1, the MK-4 content decreased significantly ($p<0.05$) in the liver of male and female fish but increased significantly in the gonad of female fish ($p<0.05$). However, no such apparent change in the MK-4 content was observed in other tissues. The reason for the marked decrease in the liver and marked increase in the gonad of the fish in Group 1 can not be presently explained. The fact that the MK-4 content in eggs decreased to a low level soon after the fish were fed with a vitamin K free diet (Fig. 13) may be related to the marked decrease in the gonadal levels (Fig. 11). Male fish began to die about 20 days after the start of the feeding experiment, seemingly coincident with the decrease of MK-4 levels in the tissue.

That a large number of immature cells were observed in the kidney of the fish fed with a vitamin K free diet suggests a high incidence of hematoporia and/or hematopoiesis in the renal tissue. Since hematopoiesis in fish is considered to occur mainly in the spleen and kidney (Branson 1993), we suggest that the vitamin K free diet brought about some changes in the level of vitamin K in the blood, and resulted in the hematopoiesis in the kidney.

The reason why only male fish died when fed with the vitamin K free diet is a matter for question. Since it is known that the hepatosomatic index of female fish is generally two to three times higher than that of male fish, and that the liver becomes extremely active in the spawning season (Tamura 1977), the death of male fish might be related to such factors. On the other hand, hatchability and mortality of larvae in this study were not affected by vitamin K deficiency. Therefore, it does not seem that vitamin K deficiency affects the growth of larvae, at least that of mummichog. It may have an effect on the physiological functions of the fish only during the spawning season. These results may suggest that mummichog requires a high level of vitamin K especialy in spawning season. However, further detailed study on the cause of death in male mummichog is needed.

3.2. The effect of dietary vitamin K (phylloquinone and menadione) levels on the vertebral formation in fish

The participation of vitamin K in fish bone development has been investigated little. One of the purpose of this section is to elucidate the effect of vitamin K deficiency on bone development in fish, using mummichog *Fundulus heteroclitus*, as an experimental animal.

A variety of naturally occurring vitamin K compounds are known. Furthermore, synthetic vitamin K exists and there are many different derivatives. They have the same naphthoquinone structure but different aliphatic side chains. MD is generally used for fish feeds as a vitamin K supplementary agent in the form of a water-soluble sodium bisulfite derivative (MSB). MD, a synthetic product of vitamin K, is not biologically active itself. The majority of MD taken in is easily excreted in rat (Losito *et al.* 1968), and only a part becomes effective after being converted into an active form, MK-4, in the liver in rat (Taggart and Matschiner 1969) and in cod (Grahl-Madsen and Lie 1997). Hence, in practice, MSB is added to feed in excess. However, it has been reported that MD and its analogues are toxic to certain animals (mice, rats, horses and humans) and cause abnormalities in the liver, kidneys and lungs, as well as hemorrhage, hemolytic anemia and other physiological abnormalities (Shimkin 1941; Smith *et*

Table 12. Composition of experimental diet

Component	Diet				
	Control	MSB25	MSB2500	PK1	PK100
Ingredient (g / kg)					
Vitamin-free casein*[1]	300	300	300	300	300
Gelatin*[2]	50	50	50	50	50
Dextrin	300	300	300	300	300
Feed oil*[3]	80	80	80	80	80
Mineral mix*[4]	40	40	40	40	40
Vitamin mix*[5]	40	40	40	40	40
Calcium lactate	0.8	0.8	0.8	0.8	0.8
Sodium phosphate, monobasic	4.8	4.8	4.8	4.8	4.8
CMC*[6]	50	50	50	50	50
Cellulose	134.4	134.4	134.4	134.4	134.4
Vitamin K (mg / kg)					
MSB*[7]	0	25	2500	0	0
Phylloquinone	0	0	0	1	100

*[1]: (Lot no. ECF7046) Wako Pure Chemical Industries (Osaka, Japan).
*[2]: DIFCO Laboratories (Detroit, USA).
*[3]: (Lot no. SNo.J-450) Riken Vitamin Company, Ltd. (Tokyo, Japan).
*[4]: Mc.Collum Salt 820517 Iwai Chemical Co., Ltd. (Tokyo, Japan).
*[5]: The premix reported by National Research Council was partly modified as follows (mg / 4 g premix): thiamin HCl 5, riboflavin 20, pyridoxine HCl 5, choline chloride 500, nicotinic acid 75, ca-pantothenate 50, inositol 200, biotin 0.5, folic acid 1.5, ascorbic acid 100, alpha-tocopherol 40, vitamin B_{12} 0.01, activated 7-dehydro-cholesterol 200IU, retinol 3200IU.
*[6]: Carboxymethylcellulose-Na.
*[7]: Menadione sodium bisulfite.

al. 1943; Owens 1971; Rebhem *et al.* 1984). In nature, fish ingest PK and/or MK-4 as the vitamin K source and it is also known that PK and MK-4, particularly PK, are accumulated by certain fish species in the liver at considerably high concentrations. However, little investigation was made in the toxicity of PK and MK to fish. The another purpose of the present study is to estimate suitable doses of PK and MSB for mummichog.

Materials and methods

Experimental diets and fish

Approximately 100 mature mummichog were fed a commercial diet supplemented with MSB in a laboratory aquarium (60L) in order to produce larvae for the experiment. Spawned and fertilized eggs were collected and kept in a fine net cage which was set in flowing natural sea water in an aquarium until hatching. Some 2000 larvae which average of body weight was 2.2mg were, divided into 5 groups of 400 each. Each group was kept in an 8L indoor aquarium. Flow rate was about 0.4L/min. The water temperature was kept at 22℃ throughout the experiment. Larvae in each group were fed for 4 weeks on experimental diets differing in vitamin K source and content. Vitamin K was not supplement to Control diet. Diet MSB25 and MSB2500 are supplemented with MSB at concentrations of 25 and 2500mg/kg, respectively. Diet PK1 and PK100 are supplemented with PK at concentrations of 1 and 100mg/kg, respectively (Table 12). These diets were given every hour between 7:00 and 18:00. Illumination of the laboratory was controlled with fluorescent lamps for thirteen-hour light photoperiod from 6:30. The experiment was run in two replicate.

Table 13. Effect of diet on the incidence of vertebral abnormalities in the skeleton after 4 weeks feeding experiment

Group	Average body weight(mg)	Mortality (%)	No. of fish			Vertebral abnormality (%)	Significance			
			Normal	Abnormal	Total		MSB25	MSB 2500	PK1	PK100
Experiment 1										
Control	6.5	19.7	75	144	219	65.8	**	-	**	**
MSB25	5.5	21.9	98	113	211	53.6		*	-	-
MSB2500	4.7	21.7	73	139	212	65.6			**	**
PK1	5.5	18.1	111	114	225	50.7				-
PK100[1)]	-	-	39	35	74	47.3				
Experiment 2										
Control	6.8	28.9	57	129	186	69.4	**	-	***	**
MSB25	7.2	19.2	100	121	221	54.8		*	-	-
MSB2500	4.8	40.6	49	95	144	66.0			**	*
PK1	6.3	29.2	90	95	185	51.4				-
PK100	4.5	27.5	86	105	191	55.0				

*Significantly different ($p<0.05$), **significantly different ($p<0.01$), ***significantly different ($p<0.001$).

[1)] Some fish were lost during the experiment.

After four weeks of rearing, all fish were starved for 20h, and 50 fish (4-week-old fish) from each group were taken for vitamin K content analysis. The 40 of 2-week-old fish and 20 of 4-week-old fish were removed out from each group, and the remaining fish were checked for vertebral abnormalities.

Observation and analysis of vertebral abnormalities

The skeletal structure was observed by double staining with alizarin red and alcian blue according to the method of Kawamura and Hosoya (1991), and examined in detail under a microscope at low magnification. All abnormal cases found were counted so as to calculate the occurrence incidence, and abnormality type was simultaneously classified. The data of abnormality were statistically analyzed by the pair-wise chi-squared tests. The abnormality type were statistically analyzed by the t-test or cochran-cox test.

Determination of the vitamin K content in fish bodies

PK and MK were determined by HPLC using a Pt column by the same method of Section 1.2.1. Fifty test fish from each group and 100 larvae immediately after hatching of each were pooled and homogenized.

Results

The incidence of abnormalities in vertebrae

The incidence of abnormalities in the vertebrae and caudal skeleton of mummichog fed diets with differing vitamin K contents in the duplicated experiments are shown in Table 13. The incidence was significantly higher in control Group fish, while the incidence in Group PK1 fish (fed a diet supplemented with PK at 1mg/kg) is considered to be low level under this study conditions. The incidence in Group PK100 fish was essentially the same as that in Group PK1, suggesting that the higher dosage of PK does not effect the incidence of vertebral abnormalities. Furthermore, the incidence in Group MSB25 fish (MSB at 25mg/kg) was also much the same as that in Group PK1. This finding suggests that the content of MSB of 25mg/kg in the feed might be appropriate. This view is also supported by vitamin K activity of MSB and its effect on bone formation (to be mentioned). In contrast to fish fed higher dose of PK (100mg/kg), fish fed higher dose of MSB showed a significantly

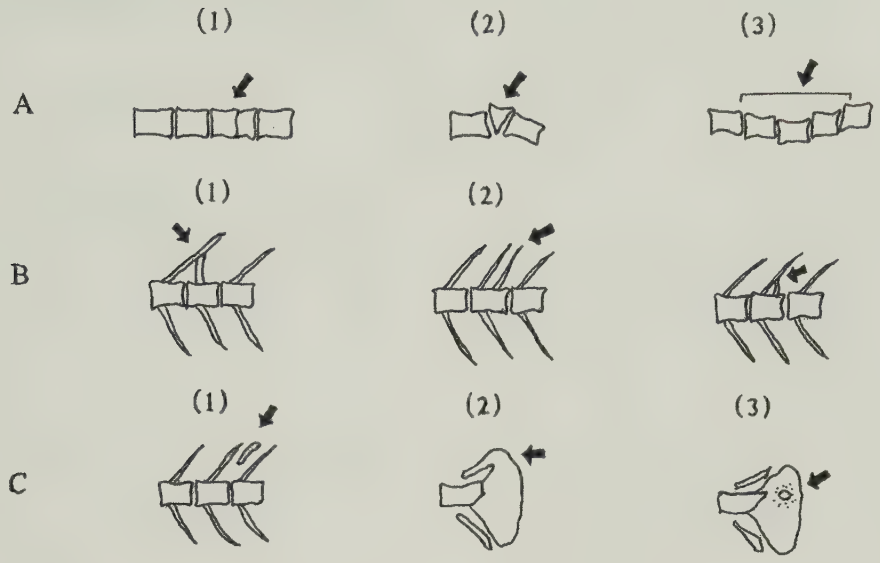
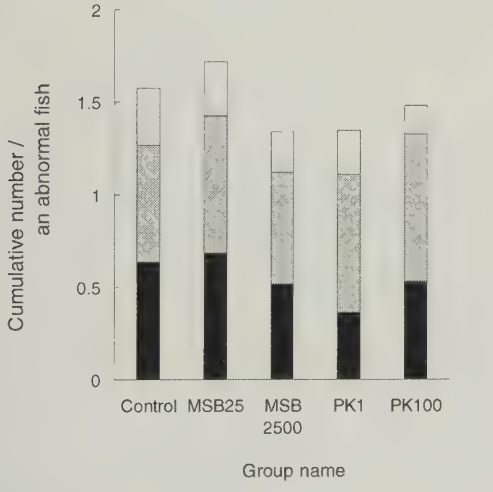


Fig. 15. Type of abnormalities in the skeleton. Arrows indicate the abnormal portion of the bones.

Type A: abnormalities in the vertebrae such as fusion occurred between adjacent vertebra (1), deformity of vertebra *per se* (2), and row irregularity of the vertebrae (3).

Type B: neural and haemal spines abnormalities such as fusion between adjacent spines (1), extra-ossification of a spine, and extra-ossification and fusion occurred (2).

Type C: abnormality differing from both Type A and Type B; for example, excessive ossicle (1), fusion of the epural to the hypural (2), and a deformity in the hypural (3).



Significance of Type A

	MSB25	MSB2500	PK1	PK100
Control	-	-	***	-
MSB25		-	**	-
MSB2500			*	-
PK1				-

* = p<0.05, ** = p<0.01, *** = p<0.001

Fig. 16. The ratio of cases of each abnormality type to the sum of cases. Solid, stippled and open bars represent type A, B and C abnormalities, respectively.

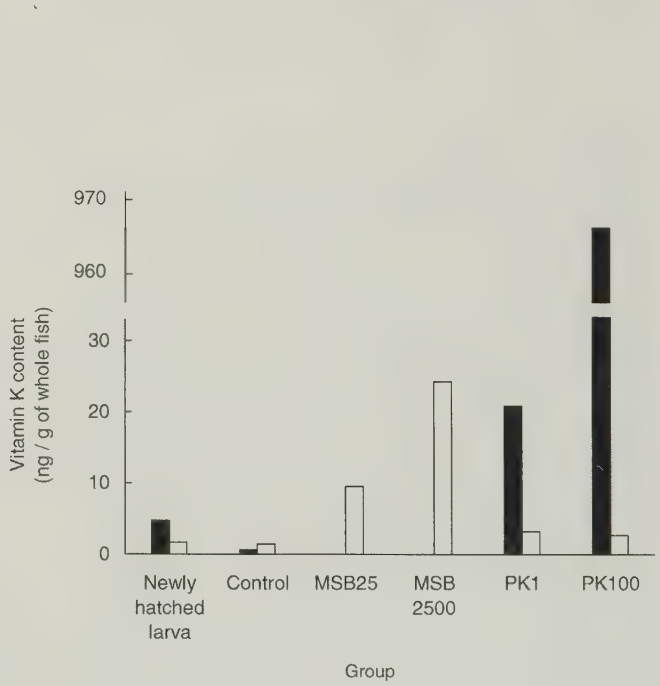


Fig. 17. Phylloquinone and menaquinone-4 contents in larvae. Solid bars represent phylloquinone and open bars represent menaquinone-4.

higher incidence of abnormalities. The mortality of fish during this experiment ranged from 18.1% to 40.6%, and did not differ significantly between the groups.

Types of abnormality

Vertebral abnormalities were classified into three types based on appearance (Fig. 15). Though it was not exact morphologically, these three types were termed types A, B and C for convenience. Type A includes abnormalities such as vertebral fusion, vertebral deformity and vertebral row irregularity. Type B comprises neural and haemal spines abnormalities such as fusion, extra-ossification and a combination of the two. Cases which could not categorized into either type A or B were lumped together under type C. The incidence of the three different types of abnormality is shown graphically in Fig. 16. The incidence of type A abnormalities is apparently high significantly in Groups Control ($p<0.001$) and MSB25 ($p<0.05$) compared to that in Groups PK1, with Group PK1 having the lowest incidence among the five groups. The incidence of type C abnormalities is relatively high in Groups Control and MSB25. However, the incidence of type B abnormalities is similar across the 5 groups.

PK and MK fish body content

Both content and form (PK or MSB) of vitamin K in experimental fish bodies were analyzed to determine differences between fish fed differing experimental diets. The results of this analysis are given in Fig. 17. The vitamin K content and form in the fish are well reflected by the experimental diets. In the newly hatched larvae analyzed for reference, a small amount of PK and a trace of MK-4 were detected. In the body of Group Control fish, only trace amounts of PK and MK-4 were found. In Groups MSB25 and MSB2500 fish, no PK and a considerable amount of MK-4 was detected. This data indicate that MSB incorporated into fish bodies was only partly, yet steadily, converted into MK-4. Even in fish exposed to a high dosage of MSB, the MK-4 level was not very high. In contrast, in Groups PK1 and PK100 fish, which were fed PK-supplemented diet, considerable amounts of PK were detected with very small amounts of MK-4. In Group PK100 fish in particular, the PK content was extremely high.

Discussion

The incidence of bone abnormalities is apparently high in fish fed with a vitamin K free diet, compared with those fed diets supplemented with PK or MSB ($p<0.01$). This result clearly indicates that vitamin K is necessary for normal bone development in mummichog as is the case for mammals. Though there is a report that many things caused bone abnormalities (Matsusato 1986), it is supposed that vitamin K is one of them.

Wild fish ingest PK as a vitamin K source, while cultured fish are generally given MSB as a vitamin K source. The effects of PK and MSB supplemented feed on bone development of mummichog larvae differ in two ways. First, when the incidence of bone abnormalities is compared between fish given either a low dose of PK (1mg/kg of diet: Group PK1) or MSB (25mg/kg of diet: Group MSB25), there is no significant difference between the two groups. On the other hand, when fish given either a high dose of PK (100mg/kg of diet: Group PK100) or MSB (2500mg/kg of diet: Group MSB2500) are compared, the incidence is significantly higher in fish given MSB than in fish given PK ($p<0.05$). Furthermore, the incidence rate between higher and lower doses of PK was not significantly different. These findings suggest that the massive dosage of MSB is harmful to bone development.

Second, the incidence of the different types of abnormalities differed between fish given a lower dose of either PK or MSB (Fig. 16). As mentioned in terms of results, MSB mainly causes type A abnormalities, namely, fusion, deformity and row irregularity of the vertebrae from PK significantly ($p<0.01$). Although it has been reported that the growth rate of cultured Atlantic salmon Salmo salar fed MSB-supplemented feed was lower than that of PK-supplemented feed (Grisdale-Helland *et al.* 1991), effect of MSB on bone development has not determined in that study. Therefore, more extensive studies on relationship between dietary MSB supplement and bone health are necessary.

The PK and MK contents in the bodies of larvae

Table 14. Composition of the experimental diet

Experimental group	Diet	
	No. 1 Group 1, 3	No. 2 Group 2, 4
Ingredient (g / 100g)		
Vitamin-free casein*[1]	30	30
Gelatin*[2]	5	5
Dextrin	30	30
Feed oil*[3]	8	8
Mineral mix*[4]	4	4
Vitamin mix*[5]	4	4
Calcium lactate	0.08	0.08
Sodium phosphate, monobasic	0.48	0.48
CMC*[6]	5	5
Cellulose	13.44	13.44
Vitamin K (mg / kg)		
Phylloquinone	-	1

*[1]: (Lot no. ECF7046) Wako Pure Chemical Industries (Osaka, Japan).

*[2]: DIFCO Laboratories (Detroit, USA).

*[3]: (Lot no. SNo. J-450) Riken Vitamin Company, Ltd. (Tokyo, Japan).

*[4]: Mc.Collum Salt 820517 Iwai Chemical Co., Ltd. (Tokyo, Japan).

*[5]: The premix reported by National Research Council was partly modified as follows (mg / 4 g premix): thiamin HCl 5, riboflavin 20, pyridoxine HCl 5, choline chloride 500, nicotinic acid 75, ca-pantothenate 50, inositol 200, biotin 0.5, folic acid 1.5, ascorbic acid 100, alpha-tocopherol 40, vitamin B_{12} 0.01, activated 7-dehydro-cholesterol 200IU, retinol 3200IU.

*[6]: Carboxymethylcellulose-Na.

differed depending on the diet fed. Figure 17 shows that a PK dose 100 times higher than that of lower dose caused a tissue PK concentration of about 50 times higher in fish, although an equivalently large dose of MSB caused only a 2.5 times increase in MK-4 concentration. In wild fish such as sardine *Sardinops melanostictus*, mackerel *Scomber japonicus* and ayu *Plecoglossus altivelis*, considerably large quantities of PK have been observed in the liver, while in cultured fish, fed a diet containing MSB, not so much MK-4 was observed. Although the reason why a large amount of PK, not MK, becomes accumulated in fish livers has not yet been elucidated, it is speculated that PK, rather than MK, plays a significant role in preventing vitamin K deficiency diseases of fish in nature.

3.3. The maternal effect of phylloquinone deficiency on bone structure in fish

The vitamin K deficient diet caused vertebral abnormality in the larvae. The effect of vitamin K deficiency of the mother fish on the eggs and larvae was not detected in term of the hatching rate and the mortality of larvae. However, the MK-4 content in eggs produced by the fish fed on the vitamin K deficient diet decreased to almost zero within the first 2 weeks. In eggs and larvae, the MK-4 contents were very low throughout the egg development period and subsequent feeding period. On the other hand, the MK-4 content in eggs spawned by fish fed on the vitamin K rich diet decreased markedly from the beginning of development and after hatching out the content became high after the first feeding.

These results indilate that vitamin K in the diet

Table 15. Abnormality after 5 days hatched out

Abnormality	Normal	Abnormal	Total	
Group 1 (Vitamin K -)	76	124	200	62.0%[a]
Group 2 (Vitamin K +)	104	96	200	48.0%[b]

Different superscripts are significantly different ($p<0.01$).

for maternal fish and after hatching out in the feed of the larvae are important to enhance vitamin K levels in the larval tissues, and that vitamin K seems to act on the bone structure. This section describes the maternal effect of vitamin K on the bone structure of the larvae. Secondly, the effects of vitamin K in the diet to larvae itself were studied.

Materials and methods

Experiment 1: Table 14 shows the diet composition. Ten pairs of parental mummichog were reared after 3 weeks being fed on No. 1 diet which is the vitamin K deficient diet. Eggs were collected from these fish and obtained as vitamin K deficient eggs. Secondly, the diet for parental fish was changed for No.2 which contains PK. After 3 weeks of rearing, eggs with a vitamin K content were obtained. The eggs layered surface seawater until hatched out, and larvae were transferred to a 20L aquarium. After 5 days, 200 larvae samples were sampled for observations on the vertebral formation.

Experiment 2 : Vitamin K deficient or contained eggs which were collected same method as in Experiment 1, were reared using the different diet respectively as in Table 14. The Group 1: the vitamin K deficient eggs fed on No. 1 diet, Group 2: vitamin K contained eggs fed on No. 2 diet, Group 3: vitamin K contained eggs fed on No. 1 diet and Group 4: vitamin K deficient egg fed on No. 2 diet. They were transferred into 20L aquaria and reared on each of diet. After 10, 15, 30 days, 200 samples were collected for observations of the vertebral formation. The skeletal structure was observed by double staining with alizarin red and alcian blue according to the method in the previous Section 3.2.

The data on abnormality were statistically analyzed by the pair-wise chi-squared tests.

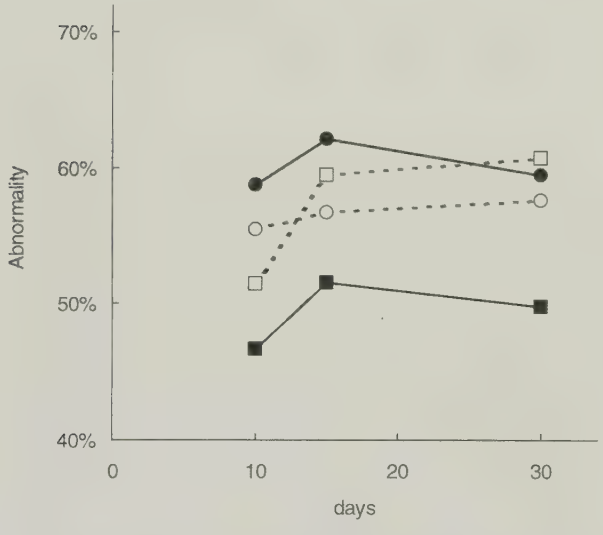


Fig. 18. Change of vertebral abnormalities in the skeleton of each group.
(●), Group 1; (■), Group 2; (□), Group 3; (○), Group 4.

Results

Table 15 shows the vertebral abnormality of mummichog after 5 days from hatching out (Experiment 1). Eggs which were fertilized from fish fed the vitamin K deficient diet showed significantly more abnormality than those from fish fed vitamin K added diet.

Fig. 18 shows the change of vertebral abnormality for each group (Experiment 2). In Group 1 fed the deficient diet, vitamin K deficient eggs produced many abnormal fish through the experiment at a level the same as after 5 days at about 60%, while in the fish of Group 2 fed the vitamin K enhanced diet, vitamin K added egg produced abnormal fish significantly less than Group 1 as same as after 5

days and abnormality was about 50%. On the other hand, Group 3 vitamin K added eggs and fed the deficient diet, abnormality increased for 15 and 30 days, so that abnormality was significantly high at 30 days the as same as for the vitamin K deficient larvae. Group 4, which were fed vitamin K added feed after spontaneous from vitamin K deficient egg, abnormality increased from 10 days to 30 days and it reached about 60%.

Discussion

Larvae which hatched out from vitamin K deficient eggs showed a significantly higher rate abnormality of the bone structure than from vitamin K rich eggs. This indicates that the maternal vitamin K content is necessary to development bone structure.

Feeding on the vitamin K deficient diet to vitamin K rich larvae led to a high rate of abnormality after 30 days. This indicates that vitamin K is necessary for bone development not only in eggs but also in the food for larvae. Vitamin K deficient eggs showed high abnormality though they were fed on vitamin K rich diet after they hatched out. This indicates that vitamin K is required in the early stage of development.

These results imply that vitamin K is necessary for the development of normal bone structure not only during production in the egg but also after hatching out.

Chapter 4. Histochemical study of the effect of vitamin K on fish bone

The precise role of vitamin K in the skeletal system is not clear. Recently, the effects of vitamin K on bone resorption and formation have been

Table 16. Composition of the experimental diet

	Diet	
Experimental group	No. 1 Group PK 0	No. 2 Group PK 1
Ingredient (g / 100g)		
Vitamin-free casein*[1]	30	30
Gelatin*[2]	5	5
Dextrin	30	30
Feed oil*[3]	8	8
Mineral mix*[4]	4	4
Vitamin mix*[5]	4	4
Calcium lactate	0.08	0.08
Sodium phosphate, monobasic	0.48	0.48
CMC*[6]	5	5
Cellulose	13.44	13.44
Vitamin K (mg / kg)		
Phylloquinone	-	1

*[1]: (Lot no. ECF7046) Wako Pure Chemical Industries (Osaka, Japan).
*[2]: DIFCO Laboratories (Detroit, USA).
*[3]: (Lot no. SNo. J-450) Riken Vitamin Company, Ltd. (Tokyo, Japan).
*[4]: Mc.Collum Salt 820517 Iwai Chemical Co., Ltd. (Tokyo, Japan).
*[5]: The premix reported by National Research Council was partly modified as follows (mg / 4 g premix): thiamin HCl 5, riboflavin 20, pyridoxine HCl 5, choline chloride 500, nicotinic acid 75, ca-pantothenate 50, inositol 200, biotin 0.5, folic acid 1.5, ascorbic acid 100, alpha-tocopherol 40, vitamin B_{12} 0.01, activated 7-dehydro-cholesterol 200IU, retinol 3200IU.
*[6]: Carboxymethylcellulose-Na.

reported (Hara *et al.* 1995). Vitamin K inhibits bone resorption and osteoclast-like multinucleate cell formation (Akiyama *et al.* 1994). Bone deformations have been reported to develop due to vitamin K deficiency in human and animals. Warfaren decreased bone resorption and bone formation strongly and caused remodeling abnormalities. In this chapter, effect of vitamin K on the fish bone resorption and fine structure are studied histochemically.

4.1. Histochemical study of the effect of vitamin K on bone development

There are reports that patients with crush fractures have very low concentrations of circulating PK (Hodges *et al.* 1993). Knapen *et al.* (1993) implied that vitamin K supplementation increases the serum markers for bone formation (including osteocalcin and bone alkaline phosphatase). These reports indicate that vitamin K functions in the bone matrix, especially the bone fine structure. The vitamin K deficient diet caused vertebral abnormality in thefish larvae. Vitamin K act as a factor in the bone mass in fish. This section describes the histochemical effect of vitamin K for the fish larvae on bone structure.

Materials and methods

Experiment 1: Table 16 shows the diet composition. Ten pairs of Mummichog *Fundulus heteroclitus* were reared after 3 weeks being fed on the vitamin K deficient diet (No. 1), and eggs were collected and obtained as vitamin K deficient eggs. Secondly, the diet was changed for the PK containing diet (No. 2) and after 3 weeks of rearing, eggs with a vitamin K content were obtained. The

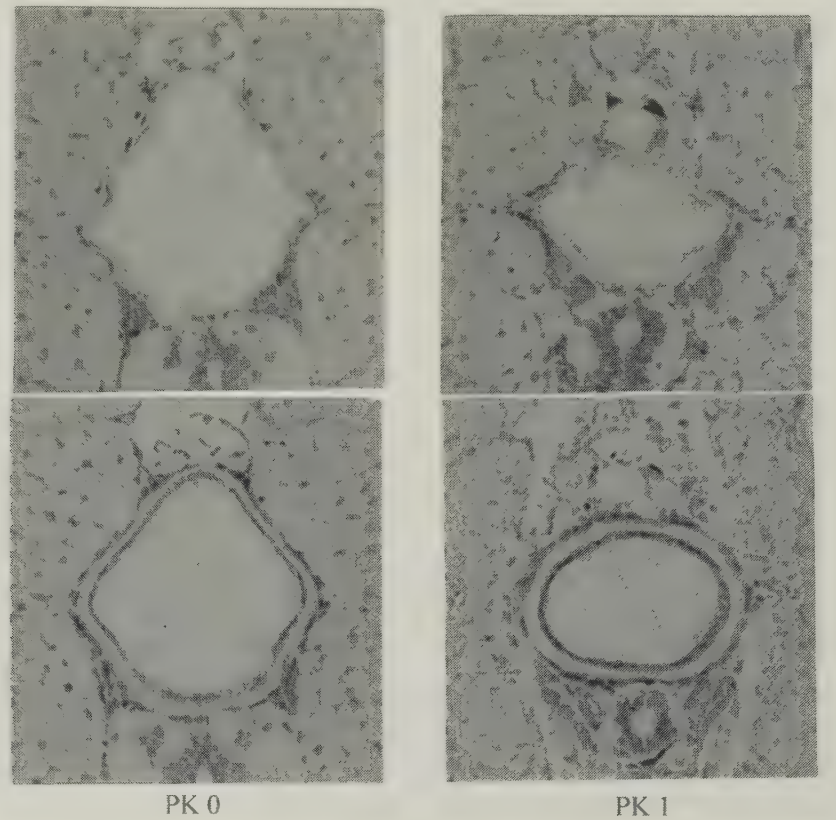


Fig. 19. Photomicrographs of cross section of vertebral bone in mummichog Fundulus heteroclitus, showing effects of vitamin K in eggs on the bone structure, 5 days after hatching. P0: vitamin K-deficient; P1:vitamin K supplemented.

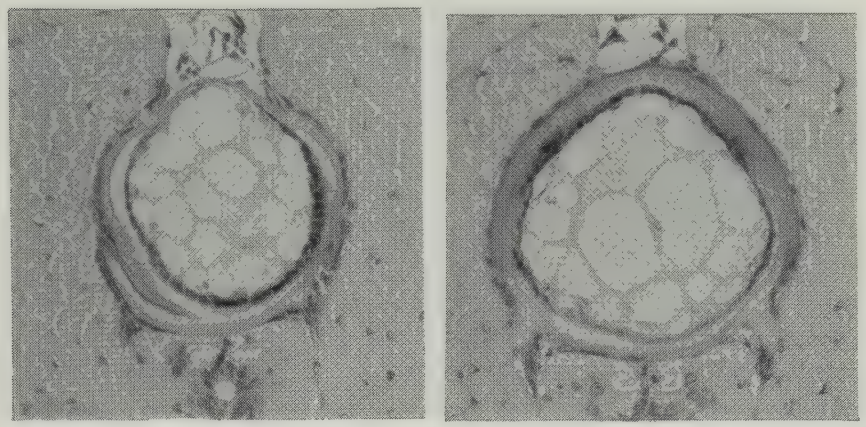


Fig. 20. Photomicrographs of cross section of vertebral bone in mummichog Fundulus heteroclitus, showing effects of vitamin K in eggs on the bone structure, 30 days after hatching. P0: vitamin K-deficient; P1:vitamin K supplemented.

eggs layered surface seawater until hatched out, and larvae were transferred to a 20L aquarium. After 5 days, the skeletal structure was observed by double staining according to the same method as detailed in Section 3.2.

Experiment 2 : Vitamin K deficient or contained eggs, which were same way as Experiment 1, were reared by the diet as Table 1. The larvae were transferred into 20 L aquaria and each reared on a diet of Group PK 0: vitamin K deficient eggs to No. 1 diet, Group PK 1: vitamin K content eggs to No. 2 diet. After 30 days, the skeletal structure was observed by double staining with alizarin red and alcian blue according to the same method as detailed in Section 3.2.

Results and discussion

Figs. 19, 20 show the observations of bone structure for the PK deficient (PK 0) and PK rich (PK 1) larvae. Fig. 19 shows the bone structure 5 days after hatching out (Experiment 1) and Fig 20 shows the bone structure 30 days after hatcheing out (Experiment 2). In the comparison of the fish bone fine structure of the Group PK 0 with that of the Group PK 1 after 5 days, the bone surface of Group PK 1 were smooth showing regular circlar but that of Group PK 0 were not constantly thick, not smooth and distorted circle. After 30 days, there was a different bone fine structure between the PK rich and the PK deficient diet larvae. The bone of the fish fed on the PK rich diet was constantly thick, while the deficient diet caused that bone was thin and rough. Thisroughness seemed that bone had been fused after being fractured finely. These results imply that PK deficient larvae had a highly decreased bone strength and formation, inducing bone structure abnormality.

4.2. Histochemical characteristics of the osteoblastic cells in fish fed a diet with vitamin K

Bone cells is a composition of osteoclasts, osteoblasts, osteocytes, and so on. Bone resorption have been incessantly, osteoclast clashes bone and osteoblast produce bone. Vitamin K deficiency caused thin and weak bones and decreases bone strength. It seemed that vitamin K deficiency decreased the bone cell activity on the bone development, and especially acts on the osteoblasts. In this section, the effects of vitamin K on the histochemical characteristics of osteoblasts were examined.

Table 17. Composition of the experimental diet

group	Control Group	Experiment Group
Ingredient (g / 100g)		
Vitamin-free casein*[1]	30	30
Gelatin*[2]	5	5
Dextrin	30	30
Feed oil*[3]	8	8
Mineral mix*[4]	4	4
Vitamin mix*[5]	4	4
Calcium lactate	0.08	0.08
Sodium phosphate, monobasic	0.48	0.48
CMC*[6]	5	5
Cellulose	13.44	13.44
Vitamin K (mg / kg)		
Phylloquinone	-	100

*[1]: (Lot no. ECF7046) Wako Pure Chemical Industries (Osaka, Japan).
*[2]: DIFCO Laboratories (Detroit, USA).
*[3]: (Lot no. SNo. J-450) Riken Vitamin Company, Ltd. (Tokyo, Japan).
*[4]: Mc.Collum Salt 820517 Iwai Chemical Co., Ltd. (Tokyo, Japan).
*[5]: The premix reported by National Research Council was partly modified as follows (mg / 4 g premix): thiamin HCl 5, riboflavin 20, pyridoxine HCl 5, choline chloride 500, nicotinic acid 75, ca-pantothenate 50, inositol 200, biotin 0.5, folic acid 1.5, ascorbic acid 100, alpha-tocopherol 40, vitamin B_{12} 0.01, activated 7-dehydro-cholesterol 200IU, retinol 3200IU.
*[6]: Carboxymethylcellulose-Na.

Materials and methods

Approximately 100 mature mummichog were fed a commercial diet supplemented with MSB in a laboratory aquarium (60L) in order to produce larvae for the experiment. Spawned and fertilized eggs were collected and kept in a fine net cage which was set in flowing natural sea water in an aquarium until hatching. Each group was kept in an 8 L indoor aquarium. Flow rate was about 0.4L/min. The water temperature was kept at 22℃ throughout the experiment. Larvae in each group were fed for 4 weeks on diets differing in vitamin K content (Table 17). Vitamin K was not supplemented to the control diet. The experimental diet was supplemented with PK at a concentration of 100mg/kg. These diets were given every hour between 7:00 and 18:00. Illumination of the laboratory was controlled with fluorescent lamps for a thirteen-hour light photoperiod from 6:30. The experiment was run in two replicates. Five of 4-week-old fish were removed from each group, and were checked for vertebral abnormalities.

The bones from the experimental fish were fixed with Bouin's fluid and embedded in paraffin. Serial sections 5 μm thick were stained with hematoxylin and eosin.

Table 18. The number of osteoblast-like cells per individual vertabral section at microscope

	Diet	
	Experiment	Control
No. 1	110	48
No. 2	62	52
No. 3	60	52
No. 4	64	52
No. 5	-	46

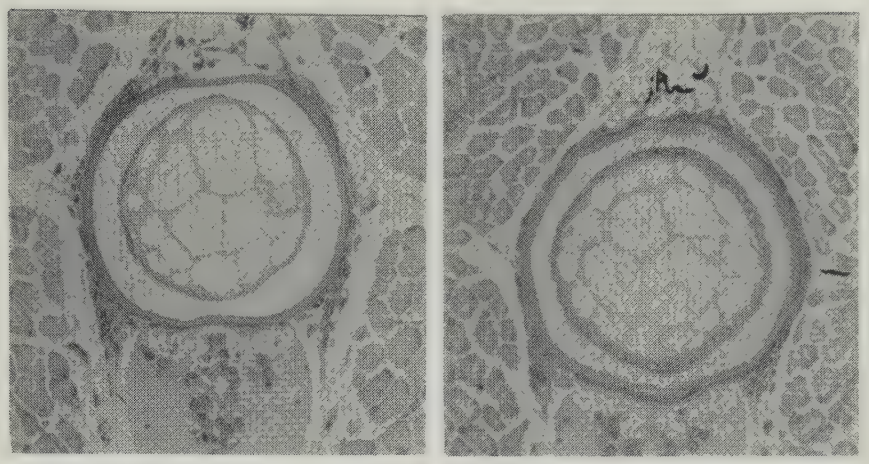


Fig. 21. Photomicrographs of cross section of vertebral bone in mummichog Fundulus heteroclitus, showing effects of vitamin K in diets on the osteoblast-like cells, vitamin K deficient.

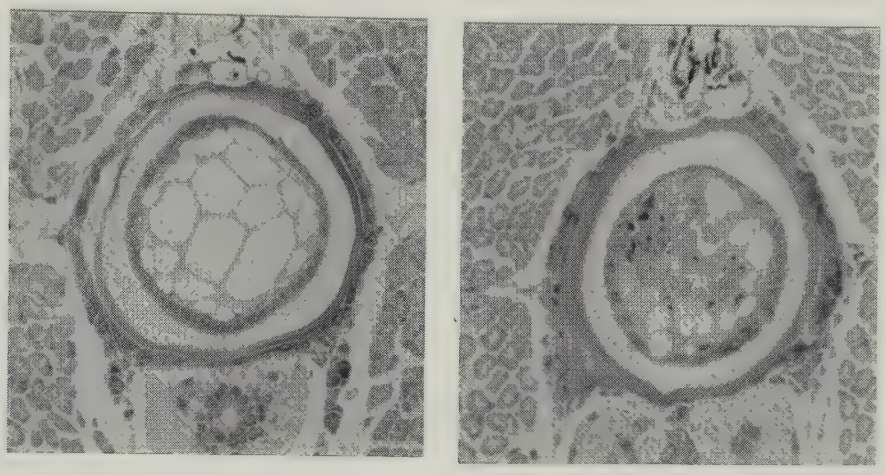


Fig. 22. Photomicrographs of cross section of vertebral bone in mummichog Fundulus heteroclitus, showing effects of vitamin K in diets on the osteoblast-like cells, vitamin K supplemented.

Results and discussion

Fig. 21, 22 show observations of the bone structure of each group. In the experimental Group, osteoblast-like cells were observed more frequently than control Group.

Table 18 shows the number of osteoblast-like cells for each group. The experimental Group, more of the osteoblast-like cells were found than the control Group. These results indicate that PK is necessary for the activation of osteoblast-like cell and a large quantity of PK activates excessive osteoblast-like cell. These data indicate that at least part of the effects of PK on bone resorption may be to regulate osteoblasts activity via an as yet unidentified mechanism.

There is a report that MK inhibits *in vivo* osteoclast formation in rats (Kawata *et al.* 1999), vitamin K may effect both osteoclast and osteoblast cells, and consequently have an effect on bone metabolism. Considering that PK is more deposited in tissue than MK, there is a possibility that PK is more useful than MK in fish differing from in mammal.

Chapter 5. Comprehensive Discussion

The contents of PK and MK-4, 6, 7, 8 and 9 in the different organs of four species of fishes were measured and compared. Mackerel, a typical pelagic fish, contained a large amount of PK but only trace amounts of MK-4 and MK-6 in the liver and kidney. Saury contained a large amount of MK-4 in the heart and gonad, and little PK. Marbled sole and sillago, demersal fish, contained relatively large amounts of MK-4 and PK but only small amounts of MK-6, 7 and 8. In marbled sole and sillago, the contents of the gastrointestinal tracts were rich in MK-long chains. While, the tissues and the digestive tracts of mackerel and saury contained low amounts of MK-long chains. In the comparison of cultured and wild ayu, the content of PK was much higher in the wild ayu, particularly in the liver, which feed on diatoms than in the cultured ayu which were fed with a commercial ayu diet. Since diatoms contain PK at a high concentration, large parts of the PK in the wild fish are considered to originate from the natural feed. Possibly, the source of vitamin K of wild ayu is considered to be the PK in the feed. On the other hand, the content of MK-4 which is known to be metabolized from menadione was high in the cultured fish. The major vitamin K in wild sardine was PK, and the stomach and intestinal contents of wild sardine as well as planktons which are consumed by the wild sardine showed a much higher level of PK than MK-4. Cultured sardine fed a MSB supplemented diet were rich in MK-4, which indicates that MD was converted to MK-4 in the body. A large quantity of long-chain MKs was found in the gastrointestinal tract content of both fish but the level was low in the tissues. These findings suggest that vitamin K in the tissues of fish originates from the food taken in and stored mainly in the liver. However, a certain discrepancy between the composition pattern of vitamin K in the tissues and contents of the gastrointestinal tract indicates that different forms of vitamin K are absorbed and/or accumulated in the tissues in a different manner. This difference suggests that the different forms of vitamin K are not equally incorporated via the metabolic system.

As feeding diets supplemented with different vitamin K groups, the vitamin K mainly detected in the gastrointestinal tract of each experimental group was the one supplemented in the respective diet, and all other forms of vitamin K were observed at low concentrations. This implies that the main vitamin K source for mummichog might be in their food, and the elevation of vitamin K concentrations in the plasma and other tissues in this experiment was brought about by the vitamin K added to the feed. The PK rich diet raised the PK concentration in the plasma and the tissues much higher than the diets supplemented with short and/or long chain MKs. This indicates that PK is more easily accumulated in the body of fish than the MK homologues. This seems to be the reason why only the PK content was higher than MKs in fish liver for sardine, mackerel and ayu. PK to MSB, a massive dose of MSB caused a high incidence of bone deformity, compared with a lower dose, while an increased dose of PK brought about no significant difference in deformity incidence. The vertebral deformity was significantly higher in fish fed a vitamin K free diet and MSB-supplemented diet compared to in fish fed a PK-supplemented diet. These results indicate that PK is more suitable than MSB as a vitamin K source in fish feed.

In mummichog reared in the spawning season on a vitamin K free diet for 11 weeks, most of the male fish died, while the female fish seldom died. In contrast, none of the male nor female fish (control fish) which were fed with a diet supplemented with MSB died. Diets without vitamin K caused a significantly higher incidence of bone deformity in fish than diets supplemented with vitamin K. These results indicate that vitamin K is essential for mummichog. The MK-4 content in the tissues markedly decreased during the experimental feeding. After 11 weeks, MK-4 was found to have accumulated in various tissues of the control fish, especially in the gonadal tissues, except for the liver. In the kidney of the female fish fed with a vitamin K free diet, a large number of immature erythrocytes were observed. This indicates that the female fish had been affected by hematoporia and/or hematopoiesis brought about by a deficiency in vitamin K. However, larval mortality was not affected by the vitamin K deficiency. These results

indicate that vitamin K intake is necessary for mummichog, particularly for the male fish during the spawning season even though they can continue to grow without any vitamin K supplement. There were apparent differences in absorption and deposition of vitamin K between females and males.

The vitamin K deficient larvae had an abnormal vertebral formation, while PK rich larvae showed a low abnormality. Vitamin K rich larvae which were fed a vitamin K rich diet after hatching had a low rate of abnormality, though one group fed vitamin K deficiency diet had high abnormality the same as larvae hatched from vitamin K deficient eggs after 30 days. On the other hand, larvae fed on a vitamin K rich diet which was hatched from vitamin K deficient egg, showed a high rate of abnormality the same as fed on vitamin K deficient diet after 30 days. These results indicate that vitamin K deficiency affects mummichog bone structure for both early development and growth.

The effect of PK on bone structure in fish were observed histochemically. The bone structure of vitamin K deficient larvae was thin and rough after 30 days feeding. It seemed to be connected after fine fracture of a bone surface. On the other hand, in larvae fed a PK rich diet this phenomenon was not observed. These results imply that vitamin K deficiency caused thin and weak bone, and it induces bone structure abnormality. Vitamin K rich diet increased the osteoblast-like cells. These results imply that PK was necessary for the activation of osteoblasts. These data indicate that at least part of the effects of PK on bone resorption may regulate osteoblasts activity via an as yet unidentified mechanism.

From these data, it can be concluded that the difference in dominant vitamin K between cultured and wild or pelagic and demersal fish is caused by differences in the food consumed by the fish. PK seemed to be absorbed more easily than MKs in the body of fish. Vitamin K deficiency causes high mortality or bone abnormality, especially PK prevents bone abnormality. It seemes to play a role in bone resorption especially on the osteoblast cells.

Chapter 6. Summary

Basic information on the distribution and role of vitamin K in fish is described in relation to dietary intake. Vitamin K in the fish tissues is mainly concentrated in the liver and gonads, with a small amount in muscle. There was a difference in the concentration of vitamin K between demersal and pelagic fish depending on the habitat and between cultured fish and wild fish. The composition and content of vitamin K in the gastrointestinal tract which were very similar to those of the food consumed differed from the tissues, suggesting that all the vitamin K in food was not transferred to the tissues of fish. There was no clear indication that vitamin K deficiency affected the growth rate or mortality in fish, although vitamin K deficiency caused histopathological changes and bone abnormalities. The vitamin K seems to have an effect on osteoblast cells. These results imply that the role of vitamin K in fish has a variety of physiological functions.

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博士号論文

Studies on fisheries and life history of *Euphausia pacifica* HANSEN off northeastern Japan[*1]

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Abstract *Euphausia pacifica* is the dominant euphausiid in the North Pacific Ocean. In the Japanese waters of the Pacific Ocean, it occurs as far south as Suruga Bay, 34° 50'N and extends northwards as far as the southwestern area of the Okhotsk Sea. *E. pacifica* is commercially exploited in Sanriku (38°－41° N) and Joban (36°－38° N) waters off northeastern Japan from late winter to early summer. The average annual catch and average annual value on landing is 66,000 ton and 3.1 billion yen, respectively, during the years 1992 and 2001. Because the annual catch, fishing period and landing value of *E. pacifica* varies between regions and years, accurate assessment of the fishery resource and prediction of fishing conditions for the next season have been demanded to maintain the stability of this fishery. On the other hand, *E. pacifica* is considered a key species because many endemic and migrant predators depend on this species as prey. In addition, the feeding impact by *E. pacifica* on the lower trophic levels in the ecosystem are significantly high considering its high biomass. Considering the important role of *E. pacifica* to transport organic matter from the lower trophic levels to higher trophic levels in the North Pacific, qualitative and quantitative analyses of distribution, life history and carbon budgets of *E. pacifica* have great importance for understanding the structure of marine ecosystems in this area. From the above mentioned reasons, the fishery, horizontal and vertical distribution, life history, biomass, carbon budgets (production and metabolism) and feeding of *E. pacifica* off northeastern Japan were examined in this study.

To examine how oceanographic conditions have affected fishing conditions, annual variations of fishing conditions such as the strength of catch and CPUE (catch per unit effort) were investigated in relation to the oceanographic conditions such as the first branch of the Oyashio Current as well as the history of development of fishing methods and regulations in *E. pacifica* fishery. The relationship between the fishing conditions and oceanographic conditions is as follows. When the first branch of the Oyashio Current is weak, fishing conditions in northernmost Iwate Prefecture are rather stable but fishing condition in Miyagi Prefecture and southernmost Joban area is unstable, showing low CPUE and delayed formation of the fishing ground. On the other hand, when the first branch of the Oyashio Current is strong, fishing conditions in Miyagi Prefecture and Joban area are favorable as well as in Iwate Prefecture, showing high CPUE and early formation of the fishing ground.

To examine the distribution and life history of *E. pacifica*, seasonal changes in spawning, distribution and growth patterns and life span of this species were investigated over a broad geographical area (mainly 36°－43° 00' N and west of 145° E) using Norpac net and cylindrical-conical net samples. Mating and spawning occurred throughout the year in the Oyashio area ($T_{100} \leqq 5$℃) and colder waters of the transitional area (5℃ $< T_{100} \leqq 10$℃, with a peak in spring but less in late fall-winter. Apparent growth was recognized from March to June for

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the small-sized group of adults. The life span of male and female *E. pacifica* off northeastern Japan was estimated to be 24 months and 28 months, respectively. *E. pacifica* gradually adapts to colder areas as the developmental stage progresses from furcilia to adults, and advanced-age adults (large-sized group of adult) rarely occur in warmer areas. Geographical distributional pattern of spawning and each stage was generally closely related to the distribution of the water masses.

To examine physical and biological factors which determine the vertical distribution of *E. pacifica*, seasonal variations of vertical distribution of *E. pacifica* were investigated in the coastal and offshore waters (36°–42° 00' N and west of 145° E), using ORI, beam-trawl and MOCNESS-I net samples. In the Sanriku coastal waters, benthopelagic *E. pacifica* occurred on the upper slope from early summer to fall where strong thermocline occurred in the middle layer above colder temperatures under 8℃ in the low layer. In spring, adult *E. pacifica* forms dense pelagic aggregations throughout the day on the continental shelf where water with 7–8℃ dominates in the total water column. In the offshore area, annual average median depth of each developmental stage of *E. pacifica* at night tended to increase with the developmental stages from middle-furcilia to large adults, while the median depth in the daytime tended to increase with developmental stages from first calyptopis to sixth furcilia. Median depth at night of immature and adult stages tended to be deeper in the warmer areas in summer and fall, especially large adults hardly reached beyond the thermocline in the mid layer. In spring, the median depth during daytime of immature and adult stages was significantly shallower than that in other months and thus the distance of diurnal vertical migration tended to be shorter.

To examine the characteristics of carbon budgets of *E. pacifica*, biomass, production and metabolism of *E. pacifica* were investigated along the coastal waters (36° 50'-42° 50'N). High biomass was found in summer-fall off southeastern Hokkaido, and in the late winter-early summer off Sanriku and Joban. Annual mean biomass was 381, 314 and 258mg C m^{-2} off southeastern Hokkaido, Sanriku and Joban, respectively. The total production (sum of growth, moults and eggs) during the survey period off southeastern Hokkaido (3,829mg C m^{-2}) was comparable with that off Sanriku (3,872mg C m^{-2}); both were much higher than that off Joban (2,243mg C m^{-2}). The somatic production during the survey period contributed to the highest proportion (51.5–70.9 %) of the total production in the respective coastal areas. The total metabolism (routine and diurnal vertical migration) during the survey period ranged from 3,846mg C m^{-2} off southeastern Hokkaido to 3,062mg C m^{-2} off Joban, accounting for 50.1–57.7% of the assimilation (production and metabolism). The routine metabolism during the survey period ranged from 2,783mg C m^{-2} off Sanriku to 2,257mg C m^{-2} off Joban, contributing the highest proportion (32.8–42.5 %) to the assimilation in each coastal area.

To examine how diets and feeding behavior change according to ambient food conditions, seasonal change in stomach contents of *E. pacifica* was surveyed in the coastal waters off southeastern Hokkaido and Joban. *E. pacifica* tended to consume many diatoms when high chlorophyll *a* concentrations occurred but tended to consume large numbers of copepods when the chlorophyll *a* concentration was low in each of the coastal areas surveyed. Both the numerical number and carbon content of copepods in the stomach of *E. pacifica* off Joban were generally higher than those off southeastern Hokkaido throughout the year. The copepod contribution to the total food ingestion for adult size of *E. pacifica* is estimated to be 7.3% and 30.0% off southeastern Hokkaido and Joban, respectively. The contribution of copepods as food of *E. pacifica* is thought to be higher in the southern warmer waters.

Finally, three key points are discussed from the results obtained in this study, in comparison with the cases of *Euphausia superba* and *Neocalanus species*, i.e. (1) significances of seasonal migration of *E. pacifica*, (2) mechanism of formation of fishing ground in *E. pacifica* in the Sanriku and Joban coastal waters, and (3) impact of feeding by *E. pacifica* on the primary and secondary production.

Key Words: distribution, *Euphausia pacifica*, fishery, life history, northeastern Japan

Contents

Chapter 1. Introduction
Chapter 2. Fishery of *Euphausia pacifica*
Materials and Methods
Results
History and present status of the *E. pacifica* fishery
Annual change in the oceanographic conditions in the Sarniku and Joban coastal waters
Annual landings and unit price
Number of krill fishing vessels
Catch
CPUE
Fishing period
Location of fishing ground from 1995 to 2001
Discussion
Development of *Euphausia pacifica* fishery
Relationship between oceanographic conditions and fishing conditions
Chapter 3. Distribution and life history of *Euphausia pacifica*
Materials and Methods
Norpac net survey
Cylindrical-conical net survey
Results
Seasonal changes in the developmental stage composition in water masses
Seasonal growth pattern and life span
Seasonal change in developmental stage composition among areas
Discussion
Seasonal change in spawning and distribution in water masses and life history
Geographical change in spawning and distribution
Spawning period during the life span
Chapter 4. Vertical distribution of *Euphausia pacifica*
Materials and Methods
Distribution of pelagic and benthopelagic *E. pacifica* in the Sanriku waters
Distribution in the offshore waters of northeastern Japan
Results
Distribution of pelagic and benthopelagic *E. pacifica* in the Sanriku coastal waters
Distribution of *E. pacifica* off northeastern Japan in April
Distribution of *E. pacifica* off northeastern Japan in July
Distribution of *E. pacifica* off northeastern Japan in September
Distribution of *E. pacifica* off northeastern Japan in November
Discussion
Characteristics of the pelagic and benthopelagic *E. pacifica* in the Sanriku coastal waters
Characteristics of seasonal horizontal distribution in the offshore waters
Diurnal vertical migration of each developmental stage
Characteristics of diurnal vertical migration of immature and adult stages
Chapter 5. Biomass, production and metabolism of *Euphausia pacifica*
Materials and Methods
Results
Biomass
Seasonal growth pattern
Production
Metabolism
Assimilation and ingestion
Discussion
Characteristics of biomass
Characteristics of production and assimilation
Chapter 6. Feeding of *Euphausia pacifica*
Materials and Methods
Results

Discussion
Chapter 7. General discussion
Significance of seasonal migration of *Euphausia pacifica* off northeastern Japan
Characteristics of formation of fishing ground of *E. pacifica*
Impact on the primary and secondary productions by ingestion of *E. pacifica* off northeastern Japan
Acknowledgements
References

Chapter 1. Introduction

Euphausiids are eucarid crustaceans and the order Euphausiacea is divided into two families, the Bentheuphausiidae containing the single genus and species *Bentheuphausia amblyops*, and the Euphausiidae containing all the other species and there are 86 known species in the order Euphausiacea (Baker *et al.*, 1990). There are currently at least six commercial fisheries harvesting six different species of euphausiids; Antarctic krill (*Euphausia superba*) which is fished off Antarctic, *Euphausia pacifica* fished off Sanriku and Joban (northeastern Japan), western Canada, *Euphausia nana* fished in Uwajima-Bay in Ehime Prefecture (southwestern Japan), *Thysanoessa inermis* fished off western Hokkaido and off eastern Canada, and *Thysanoessa raschi* and *Meganyctiphanes norvegica* fished off eastern Canada. Most of these fisheries have been in operation for over 30 years. The current world catch of all species of krill is approximately 160,000 tonnes (Nicol and Endo, 1997).

Euphausia pacifica is the dominant euphausiid in the North Pacific Ocean (Brinton, 1962; Mauchline and Fisher, 1969). In the Japanese waters of the Pacific Ocean, it occurs as far south as Suruga Bay, 34° 50'N (Sawamoto, 1992) and extends northwards as far as the southwestern area of the Okhotsk Sea (Ponomareva, 1963; Ohtsuki, 1975). It is present over almost the entire Sea of Japan extending northwards as far as the southern part of the Gulf of Tartary (Komaki and Matsue, 1958; Ponomareva, 1963). *E. pacifica* is considered a key species in the marine ecosystem off northeastern Japan because many endemic and migrant predators, including pelagic and demersal fishes, marine mammals, seabirds and benthic organisms, depend on this species for food (Nemoto, 1957, 1962; Takeuchi, 1975; Ogi and Tanaka, 1984; Odate, 1991; Nicol and Endo, 1997; Yamamura *et al.*, 1998).

Euphausia pacifica is commercially exploited in Sanriku and Joban waters from late winter to early summer. The main fishing period is from March to April, when the first branch of the Oyashio Current extends southward close to the Sanriku (38°–41°N) and Joban (36°–38°N) coasts (Komaki, 1967). Generally, the southern tip of the first branch of the Oyashio Current reaches its southernmost latitude in April and recedes to its northernmost latitude in December (Ogawa, 1989). The fishing grounds are formed near the frontal area between the coastal branch of the Oyashio Current and the coastal waters (Odate, 1991). It is generally considered that the dense population of *E. pacifica* is transported to the Sanriku and Joban coastal areas in spring by the first branch of the Oyashio Current (Odate, 1991).

So, several studies on the mechanism of formation of fishing ground and condition have been conducted (Terazaki, 1981; Odate, 1991; Kotani, 1992; Kodama, 1995a; Ebisawa, 1995). The average annual catch and landing value is 66,000 tonnes and 3.1 billion yen, respectively, during the years 1992 and 2001. But, fishery of *E. pacifca* has drastically changed historically, i.e. fishing effort and catch increased remarkable from the late 1960s; fishing methods changed drastically in the late 1980s; and several self-regulation restrictions by fishermen have been set from the early 1990s. Therefore, annual variations of fishing conditions have been closely related to social and economical reasons other than the natural variations of oceanographic conditions and the resources. Because annual catch, fishing period and landing value of *E. pacifica* varies between regions and years, fishermen and the processing industry have been demanding accurate assessment of fishery resource and prediction of fishing condition to maintain stability of this fishery.

Euphausia pacifica has seven developmental stages; egg, nauplius, metanauplius, calyptopis, furcilia, immature and adult stages. Iguchi and Ikeda (1994) showed that the egg (capsule diameter: ca. 0.4-0.5mm) development time is $<$1, 2, 4 and 7 days,

when the ambient temperatures is >15, 10, 5 and 1 ℃, respectively. According to Ross (1981), 2.0-2.2, 2.3-6.0, 13-14 and 27.5-46 days are required for the nauplius (ca. 0.3-0.5mm body length), metanauplius (ca. 0.4-0.6mm BL), calyptopis (ca. 0.8-2.2mm BL) and furcilia (ca. 1.8-6.0mm BL) stages, respectively, at the temperature conditions of 8 and 12℃. Warmer temperatures generally reduce developmental time for each stage (Ross, 1981; Iguchi and Ikeda, 1994). According to field observations at several locations, recruitment time to adult stage (> ca. 10mm BL) via larval and immature (ca. 6.0-10.0mm) stages is estimated to be ca. 3 months (Brinton, 1976; Endo, 1981; Iguchi *et al.*, 1993).

Several studies on the life history of *E. pacifica* have been conducted and have elucidated that the life history varies between regions (Nemoto, 1957; Ponomareva, 1963; Smiles and Pearcy, 1971; Brinton, 1976; Heath, 1977; Endo, 1981; Ross *et al.*, 1982; Fulton and LeBrasseur, 1984; Odate, 1991; Pogodin, 1990; Bollens *et al.*, 1992; Iguchi *et al.*, 1993; Tanasichuk, 1998a). For example, spawning occurs throughout the year and life span is estimated to be 8-12 months off warmer southern California (Brinton, 1976). While, spawning was limited in early summer and life span is estimated to be 2 years in colder Okhotsk Sea (Ponomareva, 1963). Endo (1981) reported that eggs and larvae of this species occur throughout the year in Sanriku waters, but are most abundant in April-June. He estimated the life span of females to be more than 2 years and males to be less than 2 years on the basis of length-frequency distributions. However, the distributional area of *E. pacifica* is characterized by a complex oceanographic structure represented by the Oyashio Current, Kuroshio Current Extension, Tsugaru Warm Current, and numerous warm-core rings shed by these currents (Uda, 1938; Kawai, 1972; Tomosada, 1986). The variabilities of these oceanographic processes combine to affect the distribution and abundance of euphausiids. Given the wide distributional range of *E. pacifica* as well as probable horizontal advection, large areas need to be surveyed using the same gear and methods to effectively investigate the life history of this species. To date, however, population dynamics studies of *E. pacifica* in the northwestern Pacific have been conducted at a few fixed stations (Endo, 1981; Terazaki *et al.*, 1986) or based on catches by commercial fishing boats (Komaki, 1967; Odate, 1991).

Diurnal vertical migration performs an important role to transport organic matter vertically. Several studies on diurnal vertical migration of *E. paciifca* has been conducted (Boden, 1950; Ponomareva, 1963; Brinton, 1967; Alton and Blackburn, 1972; Frost and McCrone, 1974; Marlowe and Miller, 1975; Youngbluth, 1976; Endo, 1981; Terazaki *et al.*, 1986; Bollens *et al.*, 1992; Iguchi *et al.*, 1993; Iguchi, 1995; DeRobertis *et al.*, 2000). Eggs of *E. pacifca* are usually released in the surface layers as other species of euphausiid which live in the surface layer. These eggs are thought to sink and hatch at the first nauplius in the middle layer which develops through the second nauplius into metanauplius. The mouthparts of the nauplius and matanauplius are not functional and so they presumably do not feed in the middle layer. The first calyptopis following metanauplius begins to feed using functional mouthparts in the surface euphotic layer. After calyptopis, *E. pacifica* gradually extends its vertical migration range with developmental stages (Brinton, 1967; Endo, 1981; Bollens *et al.*, 1992; Iguchi *et al.*, 1993; Iguchi, 1995). Due to their weak swimming ability, larval stages of euphausiids generally undergo diurnal vertical migration in the shallower layer in order to effectively utilize phytoplankton in the surface layer (Mauchline and Fisher, 1969; Iguchi, 1995). On the other hand, Bollens *et al.* (1992) showed that vertical distribution during daytime of furcilia stage in *E. pacifica* depended on the abundance of visual fish predators which varied between years and months in the Dabob Bay, off western USA. Endo (1981) assumed that the difference of diurnal vertical migration pattern of adult *E. pacifica* between off eastern Hokkaido, Sanriku, Yamato-tai (Japan Sea) was attributable to the development of the thermocline. On the other hand, Terazaki *et al.* (1986) showed that diurnal vertical migration of copulated females of *E. pacifica* was different from that of other individuals in Sanriku waters in spring. However, studies on the vertical distribution of *E. pacifica* off northeastern Japan has been conducted only at a few fixed stations during limited seasons.

Euphausia pacifica is important not only as the

target species of fishery but also as the food for commercial fishes in the ecosystem in the northeastern Pacific Ocean and several studies on the biomass and production of this species has been conducted there (Lasker, 1966; Heath, 1977; Mauchline, 1977; Brinton and Reid, 1986; Gomez-Gutierrez and Robinson, 1997; Tanasichuk, 1998a). The annual mean biomass of *E. pacifica* in the coastal water in the upstream California Current (Heath, 1977; Mauchline, 1977) tends to be higher than that in downstream California Current (Brinton, 1976; Gomez-Gutierrez and Robinson, 1997). The annual $P_g : B$ ratio is high (6.4–16.7) for *E. pacifica* off Barkley Sound (Tanasichuk, 1998a) that shows continuous occurrence of larvae throughout the year and high growth rates, but is low (2.6; recalculated value by Iguchi and Ikeda (1999)) for *E. pacifica* in Saanich Island (Heath, 1977). The annual production due to growth and moults of larval and immature specimens (<9mm) showed a high proportion to the total (25–72% for growth and 7–46% for moults), although their annual mean biomass showed a low proportion to the total (14–24%) from 1991 to 1997 in *E. pacifica* off Barkley Sound (Tanasichuk, 1998a). In the northwestern Pacific Ocean, however, such a study has been conducted only in Toyama Bay, Japan Sea by Iguchi and Ikeda (1999).

Considering the important role of *E. pacifica,* to transport organisms from lower trophic level to higher trophic level studies on the feeding ecology of *E. pacifica* have great importance for understanding the structure of marine ecosystems off northeastern Japan. Several studies on the feeding ecology of euphausiids have been conducted and these are generally divided into three categories; morphological studies (Ponomareva, 1963; Nemoto, 1967), laboratory experiments on ingestion (Lasker, 1966; Parsons *et al.*, 1967; Ross, 1982; Ohman, 1984; Williason and Cox, 1987; Dilling *et al.*, 1998) and stomach content analysis (Ponomareva, 1963; Endo, 1981; Nakagawa *et al.*, 2001). Nakagawa *et al.* (2001) analyzed the stomach contents of *E. pacifica* in Sanriku waters and showed that ingestion of copepods was most important to effectively acquire energy while the stomachs contained largest number of diatoms in spring when diatoms were most abundant in the ambient water. However, feeding studies of *E. pacifica* have been conducted only in Sanriku waters (Endo *et al.*, 1985; Nakagawa *et al.*, 2001) and comparison of diet and feeding behavior between different areas showing various productivities has not yet been conducted off northeastern Japan.

In **Chapter 2,** annual variations of several fishing condition indices such as catch per unit effort, first fishing day and location of fishing ground were investigated in relation to the oceanographic condition indices such as surface water temperatures and southward shift of the first branch of the Oyashio Current. In addition, the history of development of fishing methods and regulations in *E. pacifica* fishery was investigated. From these results, how annual variations of the oceanographic conditions have affected those of fishing conditions and development of *E. pacifica* fishery in Sanriku (Iwate and Miyagi prefectures) and Joban (Fukushima and Ibaraki prefectures) coastal waters was examined.

In **Chapter 3,** seasonal changes in spawning, distribution and growth pattern and life span of *E. pacifica* off northeastern Japan were investigated using Norpac net samples collected widely (mainly 36°–43°00′ N and west of 145°E) from several monthly multi-vessel line transect surveys during 10 years, and the average pattern of the distribution and life history of *E. pacifica* off northeastern Japan was examined. In addition, seasonal changes in spawning and distribution of *E. pacifica* in several fixed stations from off southeastern Hokkaido to Joban (36° 50′–42°50′N) were investigated bimonthly using cylindrical-conical nets with large mouth opening, and geographical changes of spawning and distribution of *E. pacifica* were examined in relation to water masses.

In **Chapter 4,** seasonal variations of vertical distribution of *E. pacifica* were investigated in the coastal and offshore waters off northeastern Japan. At first, seasonal variations of distribution of pelagic and benthopelagic *E. pacifica* were investigated along the coastal waters off Sanriku using ORI and beam-trawl net samples, and their trophic significance in the coastal waters ecosystem off Sanriku is discussed in light of predator-prey relationships. Secondly, seasonal variations of vertical distribution of each developmental stage of *E. pacifica* were investigated in the offshore waters off northeastern Japan using

MOCNESS-I net samples, and physical and biological factors which determine their vertical distribution of *E. pacifica* were examined.

In **Chapter 5,** biomass, production (somatic, eggs, moults) and metabolism (routine and diurnal vertical migration) of *E. pacifica* were investigated along the coastal waters off northeastern Japan, and characteristics of carbon budgets of *E. pacifica* off northeastern Japan are discussed comparing with the same species from other regions as well as other euphausiid species.

In **Chapter 6,** seasonal change in stomach contents of *E. pacifica* was surveyed in the coastal waters off southeastern Hokkaido and Joban. From the results, how diets and feeding behavior change according to ambient food conditions was examined. In addition, the significance of ingestion of copepods by *E. pacifica* was compared between the coastal waters off northeastern Japan.

In **Chapter 7 (General discussion)**, three key points are discussed from the results obtained in each chapter. At first, significances of seasonal migration of *E. pacifica* off northeastern Japan is discussed from the point of view of feeding, reproductive maturation and segregation between developmental stages, comparing with the cases in *E. superba*. Secondly, the mechanism of formation of fishing ground for *E. pacifica* in the Sanriku and Joban coastal waters is discussed in relation to its seasonal horizontal and vertical distribution pattern and physical environments. Finally, impact on the primary and secondary production by ingestion of *E. pacifica* off northeastern Japan was estimated and is discussed comparing with *Neocalanus* species.

Chapter 2. Fishery of *Euphausia pacifica*

Several studies on the *Euphausia pacifica* fishery in relation to the oceanographic conditions have been conducted (Odate, 1979; Kotani, 1992; Kodama, 1995a; Ebisawa, 1995). Odate (1979) found an inverse relationship between the southernmost latitude of the 5℃ sea surface temperature isotherms and the annual *E. pacifica* catch. Kodama (1995a) classified oceanographic patterns into three types according to the fishing conditions for *E. pacifica* in the vicinity of Kinkazan Island. However, the annual variations in fishing conditions have been affected not only by the natural environmental conditions but also by several social and economic background effects.

In this chapter, annual variations of several fishing condition indices such as catch per unit effort, first fishing day and location of fishing ground were investigated in relation to the oceanographic condition indices such as surface water temperature and southward shift of the first branch of the Oyashio Current. In addition, history of development of fishing methods and regulations in *E. pacifica* fishery was investigated. From these results, how annual variations of the oceanographic conditions have affected those of fishing conditions and development of *E. pacifica* fishery in Sanriku (Iwate and Miyagi prefectures) and Joban (Fukushima and Ibaraki prefectures) coastal waters was examined.

Materials and Methods

Landing price, number of fishing vessels and catch in each fishery port (Fig. 2-1) from 1984 to 2001 were referred to daily reports from National Federation of Fisheries Co-operative Associations, Tohoku Branch (FCA). Landing price in the total area from 1975 to 1983 were also referred to data from FCA. Landing price, number of fishing vessels and catch in each prefecture from 1984 to 2001 were referred to data from each prefectural Fisheries Experimental station (Table 2-1).

Characteristics in conditions of *Euphausia pacifica* fishery in each year were referred to 'Quick reports on fishing and oceanographic conditions' from Japan Fisheries Information Service Center. History of development in the *E. pacifica* fishery was investigated by questioning several fishermen and owners of processing industries for the fished *E. pacifica* and by referring to Odate's monograph on the fisheries biology of *E. pacifica* (Odate, 1991).

Surface temperatures for 10 day intervals in the Sanriku (38°-41°N, 142°-143°E and 38°-38.5°N, the west of 142°E) and Joban (36°-38°N, 141°-142°E) coastal areas from 1981 to 2001 were referred to the data from Japan Fisheries Information Service Center. The southernmost latitude in each month of the first branch of the Oyashio Current from 1971 to

2001 were referred to the reports on the fishing and oceanographic conditions in Tohoku area from Tohoku National Fisheries Research Institute, National Fisheries Agency (Fig. 2-2). The weekly location of fishing ground with surface temperature isotherms from 1995 to 2001 were referred to the 'Quick reports on fishing and oceanographic conditions' from Japan Fisheries Information Service Center.

Results

History and present status of the *E. pacifica* fishery

About 100 years ago, dip net fishing, which later developed into the use of bow-mounted trawl, was operated in Sanriku coastal waters for sand lance (*Ammodytes personatus*). The same method was used to harvest *Euphausia pacifica* in the mid-1940s by the fishermen of the Oshika Peninsula in Miyagi Prefecture (Odate, 1991). Fishery statistics for *E. pacifica* have been available since 1953 from the Onagawa Fish Market. The fishery had been re-

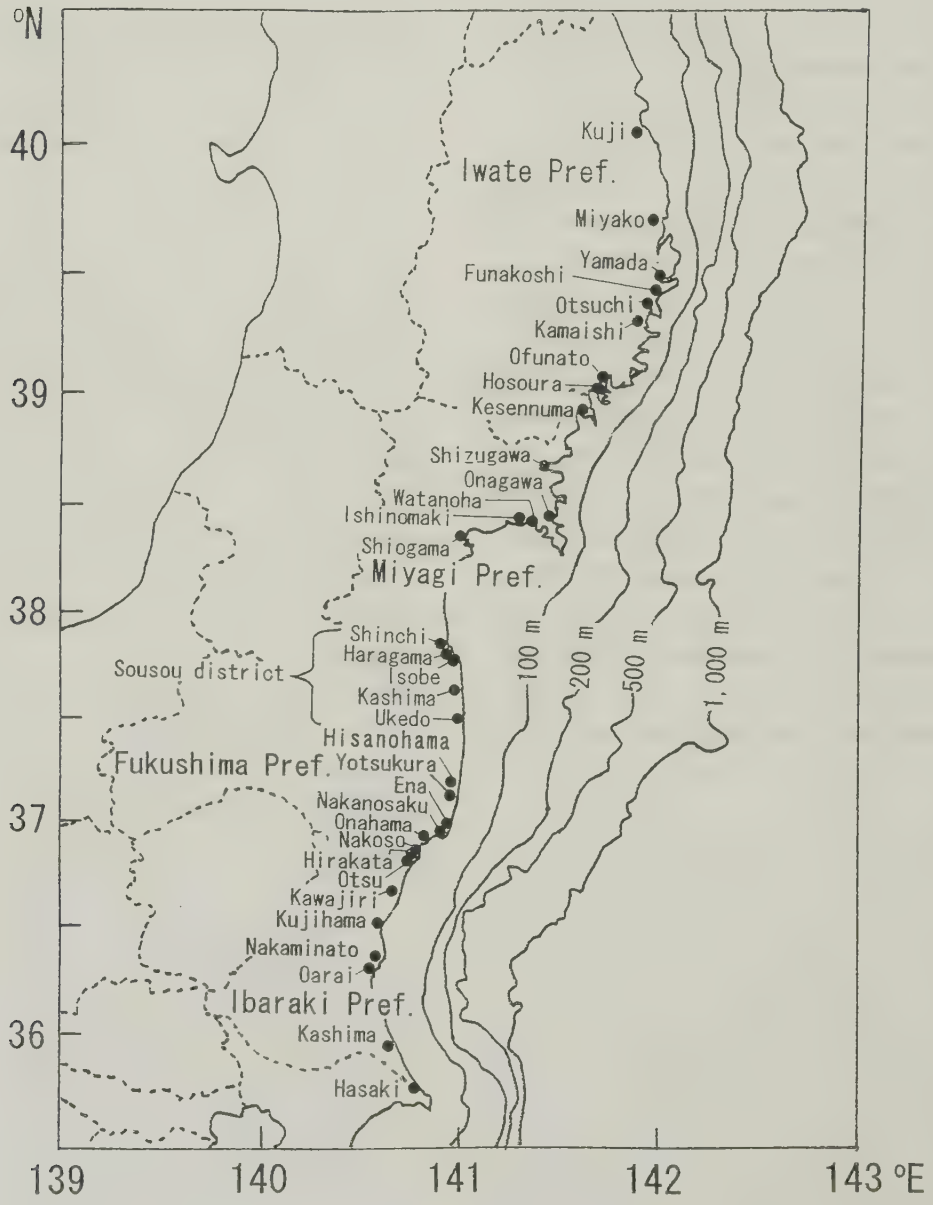

Fig. 2-1. Map of northeastern Japan indicating landing ports for *Euphausia pacifica*.

Table 2-1. References and estimation methods of fishery data

	Data	Period	Reference and method of estimation
Port	Catch	'84～'01	From FCA[*1] except '96 and '00 of Ibaraki & a part of '97 of Iwate from PRF[*2].
	Fishing days	'84～'01	Same as above.
	No. of boats	'84～'01	(*Fishing days*)/(*Fishing days no. of boats available*[*3]) × (*Available no. of boats*)
	No. of boats per day	'84～'01	(*Available no. of boats*)/(*Fishing days no. of boats available*)
	CPUE	'84～'01	(*Total catch over the days no. of boats available*)/(*Available no. of boats*)
Prefecture	Price	'84～'01	Iwate: From PRF except '84–'91 from FCA. Miyagi: From PRF except '84 from FCA. Fukushima: From PRF. Ibaraki: From PRF except '84–'91 from FCA.
	Catch	'71～'01	Iwate: From PRF except '75～'88 from Odate (1991). Miyagi: From PRF except '71～'84 from Odate (1991). Fukushima: From PRF. Ibaraki: From PRF except '72～'76 from Odate (1991).
	Fishing days	'84～'01	From FCA except '96 & '00 of Ibaraki and a part of '97 for Iwate from PRF.
	No. of boats	'84～'01	Iwate: From PRF except '84–'91 and '99 estimated by summing no. of port boats (est. from 3rd raw of table) over pref. from FCA. Miyagi: From PRF except '84 estimated by summing no. of port boats over pref. from FCA. Fukushima: From PRF except '84–'86 estimated by summing no. of port boats over pref. from FCA. Ibaraki: From PRF except '84–'91 estimated by summing no. of port boats over pref. from FCA.
	No. of boats per day	'84～'01	(*No. of boats*)/(*Fishing days*)
	CPUE	'84～'01	(*Catch*)/(*No. of boats*) but, if (*No. of boats*) was estimated from FCA as shown on the 9th raw of table, any (*catch*) is estimated by summing no. of port boats over each pref. from FCA.

[*1]Daily reports on fishery data for each port from National Federation of Fisheries Co-operative Associations, Tohoku Branch from 1984 to 2001 (except for Ofunato). Fishery data for Ofunato from 1984 to 1991 referred to from the daily reports of the Ofunato Fishery Market.

[*2]Data of Iwate Prefectural Fisheries Technical Center, Miyagi Prefecture Fisheries Research and Development Center, Fukushima Prefectural Fisheries Experimental Station and Ibaraki Prefectural Fisheries Experimental Station.

[*3]The port catch was always recorded on the fishing day, but no. of boats at ports was sometimes not recorded on the same day by FCA or PRF ('96 of Iwate).

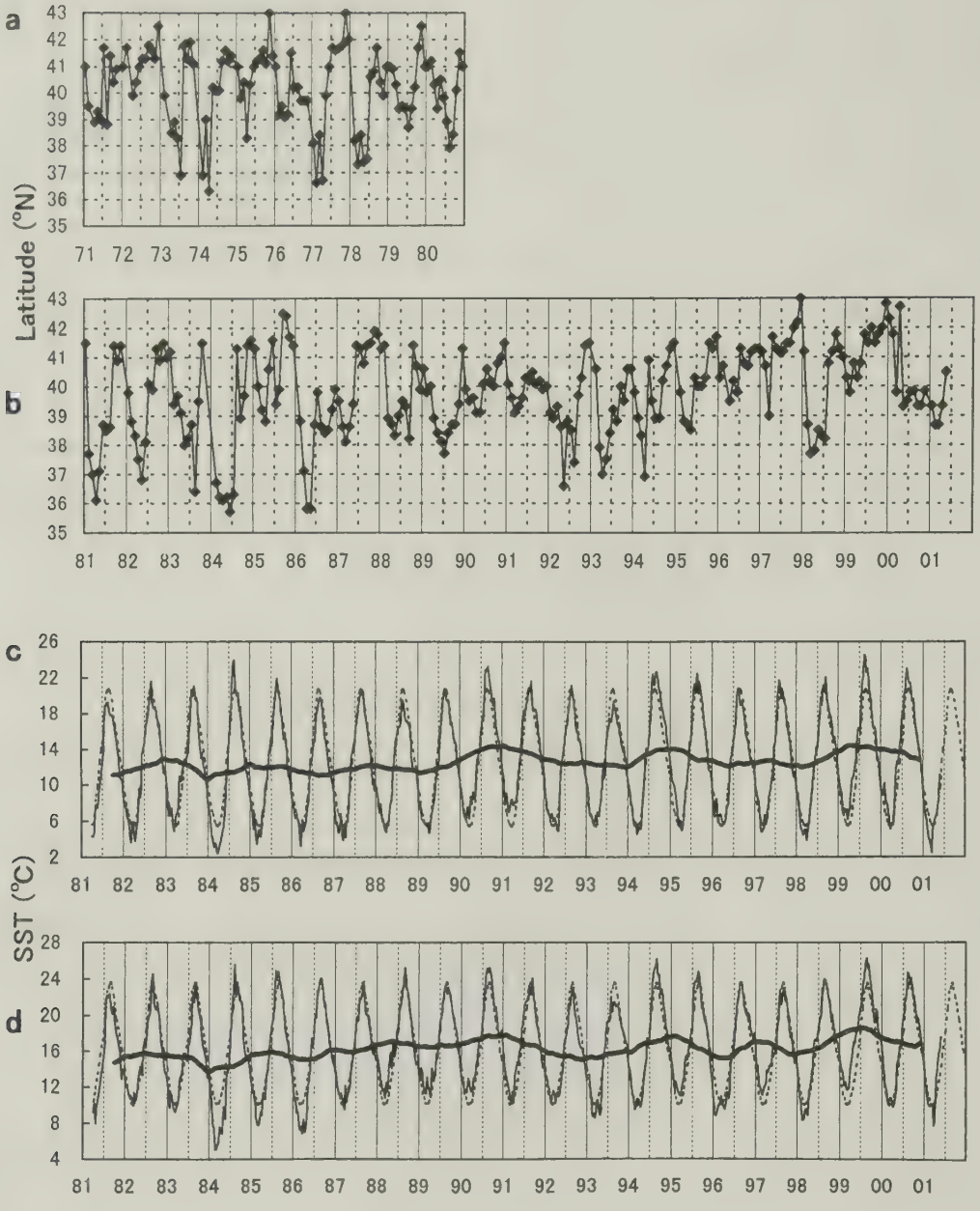

Fig. 2-2. The southern limits in each month of the first branch of the Oyashio Current from 1971 to 1980 (a) and from 1981 to 2001 (b), and the surface water temperature (SST) in the Sanriku (c) and Joban (d) waters. The southern limits of the first branch of the Oyashio Current are based on the data from the Tohoku National Fisheries Research Institute. SST is based on data from the Japan Fisheries Information Service Center. The solid thin lines, broken thin ones and solid thick ones in (c) and (d) show the raw data, mean values of the last 21 years and the 12-month running mean, respectively.

quired for a small demand for direct human consumption and for culture baits only from the local area until the 1960s.

The increased requirement for sea bream culture and bait for sport fishing in the late-1960s caused an expansion in the fishery to the north as well as along the southern coasts of Miyagi Prefecture. In Ibaraki Prefecture, fishing for *E. pacifica* began in 1972. Shortly thereafter in 1974, Fukushima Prefecture began an *E. pacifica* fishery to be followed by Iwate Prefecture in 1975 (Table 2-2).

Fished *E. pacifica* were stored in the fish hold in bulk and held in bamboo baskets until 1975. However, since 1975 plastic container which holds about 30kg of *E. pacifica* was introduced and helped reduce the rate of deterioration (Odate, 1991). Furthermore, high-speed fishing boats and effective fishing gear, such as fish pumps, echo-sounders, sonar and larger net haulers were introduced from the late 1970s to 1980s.

In Joban coastal waters, bow-mounted trawls which target the surface swarms of *E. pacifica* were adopted as well as in Sanriku coastal waters in the 1970s, but seine boats were introduced to detect benthopelagic swarms since the 1980s. The fishery to target benthopelagic swarms was established in 1985 in Joban coastal waters (Ishikawa, 1990). In Iwate Prefecture, bow-mounted trawls were adopted initially but the fishery efficiency was less efficient than in Miyagi Prefecture because the vessels were used alongside for squid fishing and were not specially designed for krill fishing as designed in Miyagi Prefecture (Minato, pers. comm.). In Miyagi Prefecture, bow-mounted trawls have been conventionally used, but seine boats were introduced in 1991 and became the main fishing method since 1992.

Therefore, seine boats are currently used in all prefectures, including Miyagi Prefecture, where they have been used alongside bow-mounted trawls since 1991. Only small boats of less than 20 tonnes GRT are engaged in the fishery. Bow-mounted trawls, which have a net opening of approximately 75m^2, only catch aggregations within 8m of the surface. In this method, when an aggregation is sighted, the boat approaches and two poles slide forward like probing antennae. The booms tilt and plunge, causing the net to spread open beneath the bow. The boat pushes the net slowly through the aggregation, engulfing the krill (Kodama, 1995b). Seine boats, the other fishing method, can catch aggregations as deep as 150m. When an aggregation is detected, a buoy fixed to the free end of a rope is thrown overboard, and the wing net, 100m long by 50m high, pocket net and second wing net are streamed out to surround the krill aggregation. After the buoy has been retrieved, both ropes are hauled whilst ensuring that the vessel orientates downwind and down current (Kodama, 1995a).

The fishing grounds lie usually over the continental shelf (<200m) within 10-20 nautical miles of the shore. Fishing operations are restricted to the daytime for two reasons. Firstly, because ports are only open during the daytime, and secondly, because fishing vessels are not equipped with freezing facilities and so they must return within a day for onshore processing and freezing of their catch (Odate, 1991). The fishing season lasts generally from February to July, but varies from area to area and from year to year. The main fishing season in Sanriku waters is from March to April. That of Joban waters is from May to June (Odate, 1991).

The *E. pacifica* fishery is categorized as a licensed fishery, licenses being issued by the prefectural governor. Fishery regulations are set separately for each prefecture. The license of the prefectural governor defines the fishing period, the time allowed at sea before the vessel must return to port (also referred to as the operational time), fishing area, boat size and other factors (Table 2-3). Other regulations which are decided by the fishermen themselves include total catch limit for the season and the maximum number of plastic containers permitted for each boat. In 1993, the total catch decreased remarkably to 60,881 tonnes as compared to the highest one (107,566 tonnes) in the previous year. That was the result of the introduction of catch regulations which were imposed in Miyagi and Iwate prefectures in order to control the market and obviate a decline in value of the catch. In 1994, catch regulations were introduced in Fukushima and Ibaraki prefectures in concert with those of Sanriku.

Annual change in the oceanographic conditions in the Sarniku and Joban coastal waters

The oceanographic conditions can be divided into

Table 2-2. Development and regulation of the *Euphausia pacifica* fishery

	Sanriku coastal waters (Iwate & Miyagi)	Joban coastal waters (Fukushima & Ibaraki)
1970	Fishery ground expanded from north to south along the coastal waters of Miyagi.	
		Fishery with seine boats commenced along Ibraki coast (1972).
1975	Fishery commenced using bow-mounted trawls in Iwate (1975). Fish-pumps were introduced in Miyagi.	Fishery with seine boats commenced along Fukushima coast (1974). Plastic catch containers were introduced in Ibraraki.
	Hydroacoustics were introduced.	
		Hydroacoustics were introduced.
1980	Seine boats were introduced along the southern coast of Iwate.	
		Benthopelagic swarms targeted for first time along coastal waters of Ibaraki.
1985		
		Benthopelagic swarms were commonly targeted.
	Seine boats commonly adopted along entire coast of Iwate.	
1990	Fishermen in Iwate set self-regulation on the max. no. of containers per boat (1990). Seine boats were permitted and adopted in Miyagi Pref. (1991). Fishermen in Miyagi set self-regulation restrictions (1991). Fishermen set self-regulation restrictions on total catch for each pref. (1993).	Fishermen set self-regulation restrictions on landing time and max. no. of containers per boat (1989).
1995		Fishermen set self-regulation restrictions in concert with those of Sanriku on the total catch for each pref. (1994).

Table 2-3. Regulatory measures of the *Euphausia pacifica* fishery from 1993 to 2001

	Iwate	Miyagi	Fukushima	Ibaraki
1993	①25,000 t ②12 t for boat > 9 t 9 t for boat <9 t ③1 Feb.–30 Apr.	①Sb[*1]: 21,000 t, Bmt[*2]: 4,000 t ②10.5 t for boat > 15 t 9.6 t for boat =10–15 t, 9 t for boat < 9 t ③Sb: 22 Feb.–30 Apr., Bmt: 1 Feb.–31 May	①No regulation ②6 t ③*1 Feb.–31 Jul.*	①No regulation ②6 t ③*11 Feb.–31 Jul.*
1994	①28,500 t ②15 t for boat > 9 t 11.4 t for boat < 9 t ③*Year round*	①28,500 t Minimum reserved[*3] for Bmt: 2,000 t ②10.5 t for boat > 15 t 9.6 t for boat =10–15 t, 9 t for boat < 9 t ③Sb: 20 Feb.–30 Apr., Bmt: 1 Feb.–30 Apr.	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1995	①28,500 t ②15 t for boat > 9 t 11.4 t for boat < 9 t ③*Year round*	①31,000 t Minimum reserved for Bmt: 4,000 t ②9 t for boat > 10 t, 8.4 t for boat < 10 t ③Sb: 1 Mar.–30 Apr., Bmt: 1 Mar.–13 May	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1996	①28,500 t ②15 t for boat > 9 t 11.4 t for boat < 9 t ③*Year round*	①32,500 t Minimum reserved for Bmt: 4,000 t ②9.6 t for boat >10 t, 9 t for boat < 10 t ③Sb; 15 Feb.–13 May, Bmt: 1 Mar.–11 May	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1997	①28,500 t ②12 t for boat > 9 t 9 t for boat <9 t ③*Year round*	①32,500 t Minimum reserved for Bmt: 4,000 t ②10.5 t for boat > 10 t, 9.9 t for boat < 10 t ③Sb: 75 days from the first fishing day Bmt: 1 Feb.–30 Jun.	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1998	①30,000 t ②12 t for boat > 9 t 9 t for boat <9 t ③*Year round*	①32,500 t Minimum reserved for Bmt: 4,000 t ②10.5 t for boat > 10 t, 9.9 t for boat < 10 t ③Sb: 75 days from the first fishing day Bmt: 25 Feb.–31 May	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
1999	①29,000 t ②10.5 t for boat > 9 t 8.25 t for boat < 9 t ③*Year round*	①29,000 t Minimum reserved for Bmt: 200 t ②10.5 t for boat > 10 t, 9.9 t for boat < 10 t ③Sb: 75 days from the first fishing day Bmt: 1 Mar.–31 May	①10,500 t ②6 t ③*1 Feb.–31 Jul.*	①10,500 t ②6 t ③*11 Feb.–31 Jul.*
2000	①29,000 t ②7.5 t for boat > 9 t 6 t for boat < 9 t ③*Year round*	①29,000 t Minimum reserved for Bmt: 200 t ②10.5 t for boat > 10 t, 9.9 t for boat <10 t ③Sb: 1 Mar.–13 May, Bmt: 21 Feb.–23 May	①9,000 t ②6 t ③*1 Feb.–31 Jul.*	①9,000 t ②6 t ③*11 Feb.–31 Jul.*
2001	①22,500 t ②7.5 t for boat > 9 t 6 t for boat < 9 t ③*Year round*	①22,500 t ②9 t for boat >10 t, 7.8 t for boat < 10 t ③Sb: 1 Mar.–14 May, Bmt: 1 Mar.–14 May	①7,000 t ②6 t ③*1 Feb.–31 Jul.*	①7,000 t ②6 t ③*11 Feb.–31 Jul.*

①: Total catch, ②: Max. no. of landings per boat, ③: Fishing period
② & ③ were alternated according to fishery and market conditions during the fishing period.
Italics: licenses issued by prefectural govenors
[*1]Seine boats, [*2]Bow-mounted trawls
[*3]Minimum reserved for dip net catch was transferred to seine boats when surface swarm disappeared in Miyagi Prefecture.

three groups according to the southernmost latitude of the first branch of the Oyashio Current (shortened hereafter as SFO) during February and July (fishing period) of *E. pacifica* as follows. The years 1973, 1974, 1977, 1978, 1981, 1982, 1984, 1986, 1989, 1992–1994 and 1998 were southward anomaly years with SFO during February and July being south of 37.7°N. The years 1975, 1979, 1983, 1987, 1988, 1995 and 2001 were intermediate years with SFO during February and July being 37.8°～38.7°N. The years 1971, 1972, 1976, 1980, 1985, 1990, 1991, 1996, 1997, 1999 and 2000 were northward anomaly years with SFO during February and July

On the other hand, the oceanographic conditions in the Sanriku coastal waters can be divided into three groups according to the trend of surface water temperatures during February and July as colder years (1981, 1982, 1984–1987, 1998 and 2001), intermediate years (1983, 1988, 1989, 1992–1997 and 2000) and warmer years (1990, 1991 and 1999) (Fig. 2-2). The oceanographic conditions in the Joban coastal waters can be divided into three groups according to the trend of surface water temperatures during February and July as colder years (1981, 1983-1986, 1993, 1996, 1998 and 2001), intermediate years (1982, 1987, 1991, 1992, 1994 and 2000) and warmer years (1988-1990, 1995, 1997 and 1999).

Annual landing values and unit price

Annual total landing of the *E. pacifica* fishery in the total area fluctuated largely from 1975 to 2001 (Fig. 2-3). It tended to increase from 1975 to 1983 and attained the maximum (4,859 million yen) in 1983. It was also higher than 4,000 million yen in 1985, 1989, 1996, 1997 and 2000, but much lower than 2,000 million yen in 1984, 1993 and 2001.

Annual landing in Iwate Prefecture increased significantly from 1987 to 1989 and attained 1,282 million yen in 1989. Since then, it has been generally higher than 1,000 million yen and attained the maximum (2,160 million yen) in 1997. Annual landing of bow-mounted trawls in Miyagi Prefecture attained the maximum (1,745 million yen) in 1987 but decreased rapidly after that and has been lower than 300 million yen since 1991. On the other hand, annual landing of the seine boats in Miyagi Prefecture has been generally higher than the average value of bow-mounted trawls from 1984 to 1990 and attained the maximum (2,239 million yen) in 1997. Annual landing in Fukushima and Ibaraki prefectures attained the maximum (1,040 and 2,177 million yen, respectively) but has been lower than 500 million yen since 1990. Therefore, the annual landing of bow-mounted trawls in Miyagi Prefecture and seine boats in Fukushima and Ibaraki prefectures had been dominant to the total form 1984 to 1988, but the annual landing of seine boats in Iwate and Miyagi prefectures had been dominant to the total since 1991.

Annual unit price fluctuated largely in each prefecture, especially in Fukushima and Ibaraki prefectures from 1984 to 1988. For example, it was 21 yen per kg in 1984 but 138 yen in 1988 in Ibaraki Prefecture. The annual unit price in Iwate Prefecture (35 yen per kg) was about 100 yen cheaper than that in Ibaraki Prefecture in 1988. This was due to strong demands for the fished *E. pacifica* in mid-June when the fishing ground in the Joban coastal waters had formed for the first time in this year after the end of fishing operation in the Sanriku coastal waters in late April (Odate, 1991). Since 1989, the annual unit price in Fukushima and Ibaraki prefectures was lower than that in Iwate and Miyagi prefectures but the annual change of unit price in the former prefectures synchronized well with that in the latter prefectures. This was because that the unit price in the Joban coastal waters had depended largely on the unit price in the Sanriku coastal waters since 1989 when the major part of fishing ground shifted to the Sanriku coastal waters as detailed below. Average annual price during 1991 and 2001 was 49 yen per kg in Iwate Prefecture, 51 yen per kg in Miyagi Prefecture, 40 yen per kg in Fukushima Prefecture and 36 yen per kg in Ibaraki Prefecture, thus being about 10 yen cheaper in the latter two prefectures than in the former two prefectures.

Number of krill fishing vessels

Annual number of fishing vessels in Iwate Prefecture increased remarkably from 1986 (859 vessels) to 1992 (5,807 vessels) (Fig. 2-4). After that, it decreased until 1994 (3,831 vessels) but increased again from 1994 to 1998 (6,177 vessels), and then decreased again after 1998. Annual number of ves-

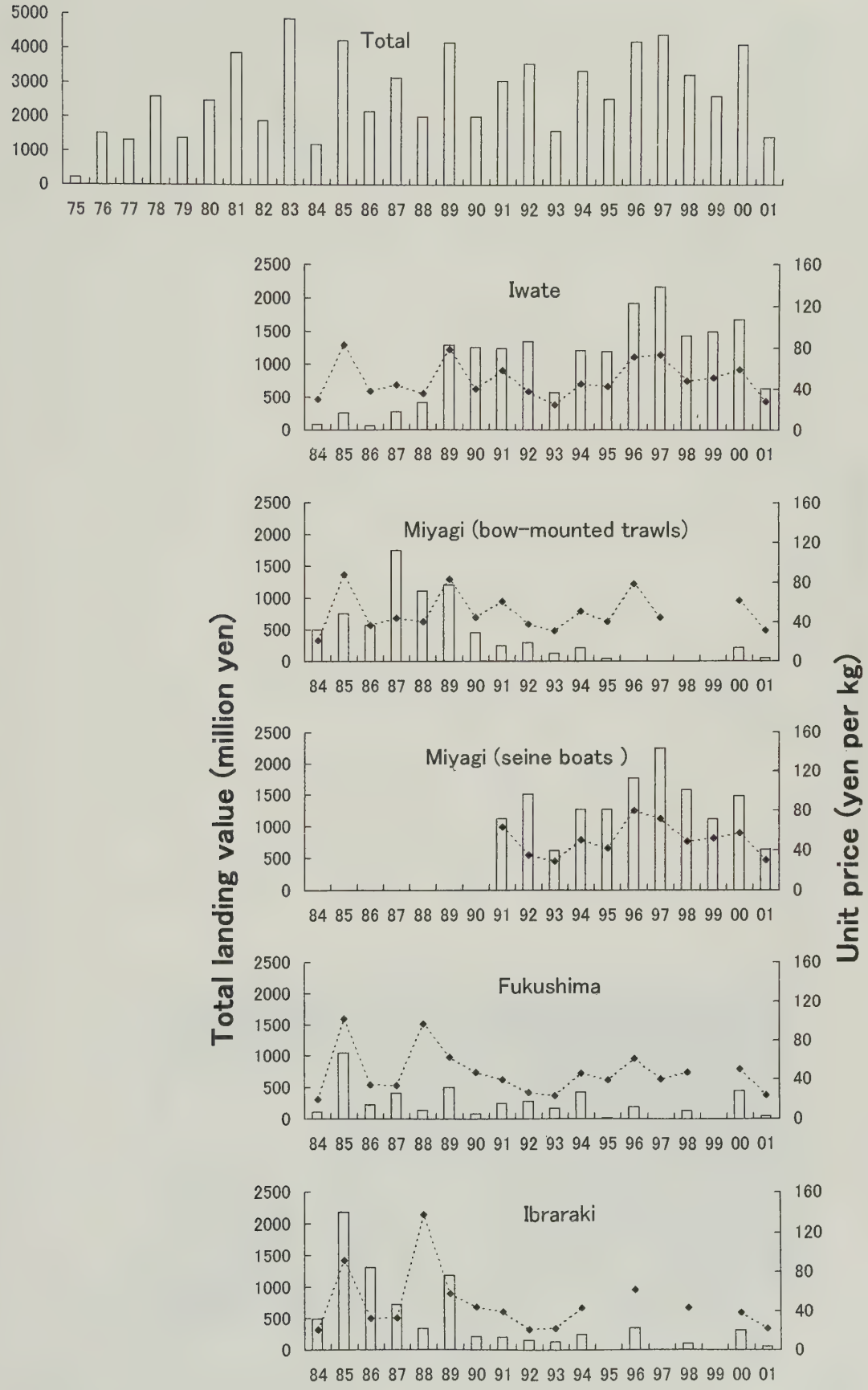
Total
Iwate
Miyagi (bow-mounted trawls)
Miyagi (seine boats)
Fukushima
Ibraraki
Total landing value (million yen)
Unit price (yen per kg)
75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 00 01

Fig. 2-3. Annual variations in the total value (bars) and unit price (broken lines) of *Euphausia pacifica* fishery by prefecture.

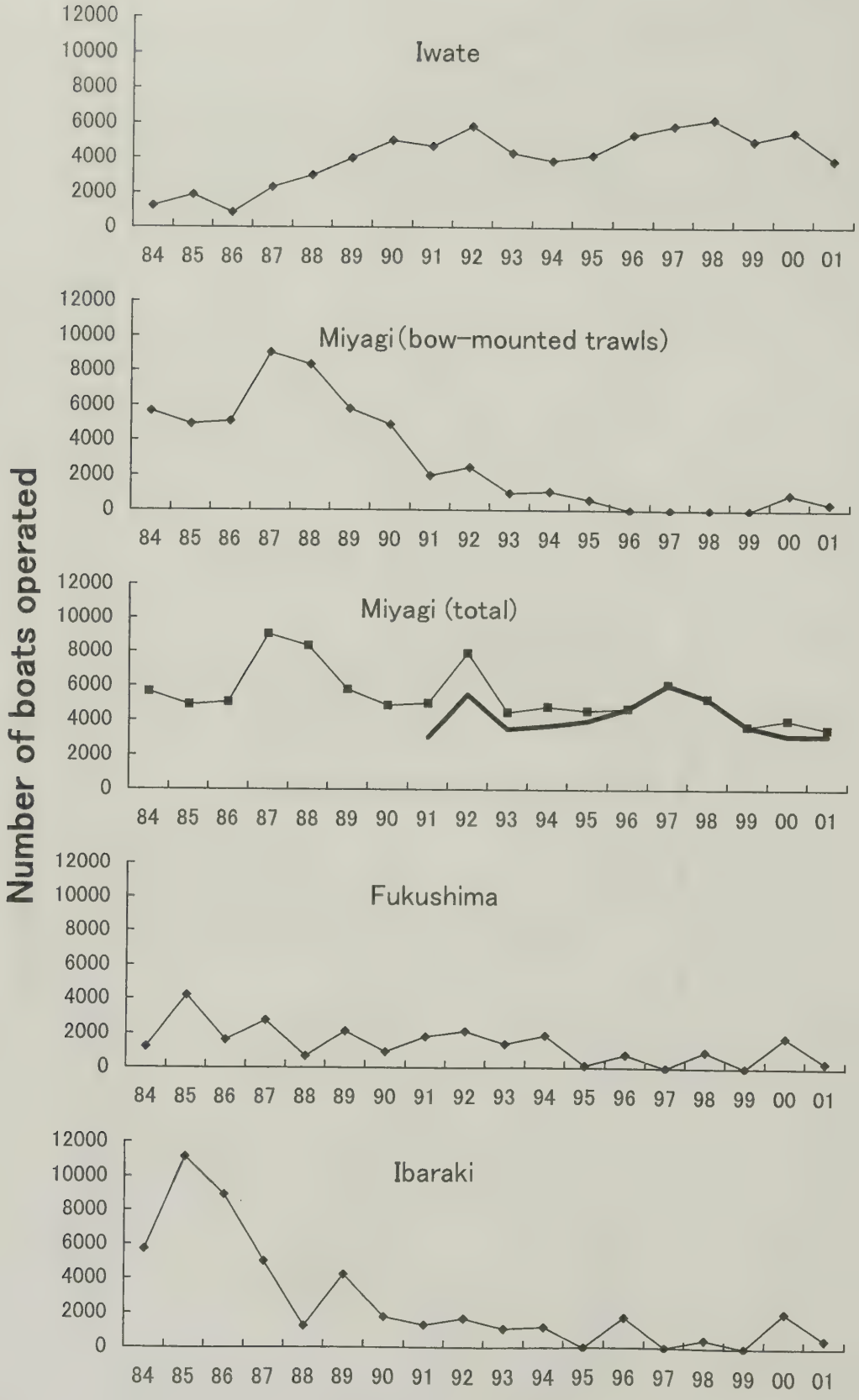

Fig. 2-4. Annual variations in the number of boats in each prefecture. Thick line shown in the panel of Miyagi (total) indicates the number of seine boats.

sels by bow-mounted trawls in Miyagi Prefecture attained the maximum (9,006 vessels) in 1987 but decreased after that and has been generally lower than 1,000 vessels since 1993. Annual number of seine boats in Miyagi Prefecture ranged from 3,019 to 6,060 vessels after 1991 when this fishing method was adopted for the first time. The relative contribution in number of seine boats to the total vessels in Miyagi Prefecture was 61% in 1991, 69% in 1992 and 77-100% after 1993. Annual number of seine boats in Fukushima Prefecture attained the maximum (4,202 vessels) in 1985 but decreased since then and has been generally lower than 2,000 vessels after 1990. Annual number of seine boats in Ibaraki Prefecture attained the maximum (11,119 vessels) in 1985 but decreased since then and has been generally lower than 2,000 vessels after 1991.

Catch

The total annual catch of *E. pacifica* varied between years but tended to increase steadily from mid-1970 to 1992 exceeding 40,000 tonnes in 1978, 80,000 tonnes in 1989 and 100,000 tonnes in 1992 (Fig. 2-5). In 1993, the total catch decreased to 60,881 tonnes, following the introduction of catch regulations which were imposed in Miyagi and Iwate prefectures in order to control the market and obviate a decline in price of the catch. Since then, the total annual catch had been around 60,000 tonnes.

Most of the catch in the 1970s was landed in Mi-

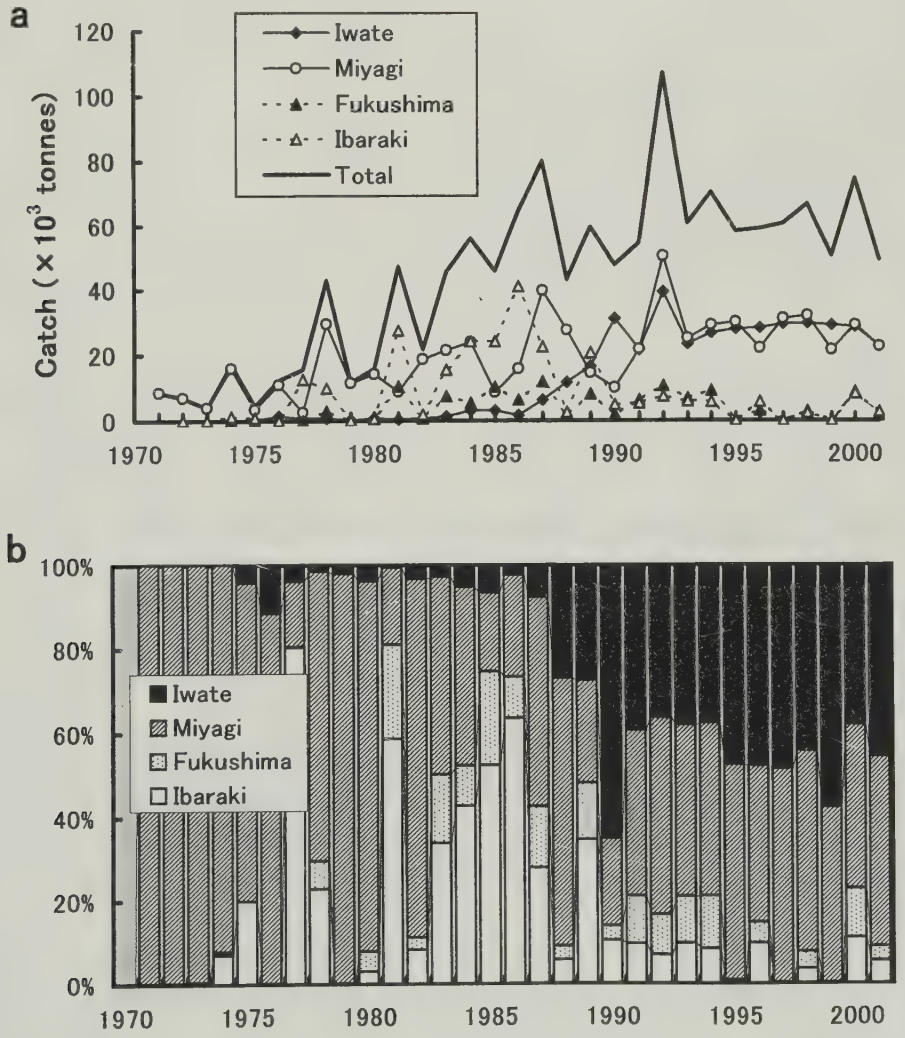

Fig. 2-5. Annual variations in the catch (a) and the percentage composition by prefecture (b) from 1971 to 2001.

yagi Prefecture (Fig. 2-5). In the early to mid-1980s, Ibaraki Prefecture expanded its catch taking more than 60% of the total catch in 1986. Since 1990, Iwate and Miyagi prefectures have shown similar catch levels and the sum of their catch showed a high percentage (79-100%) to the total. There were no catch or nearly no catch in Fukushima Prefecture in 1999 and Ibaraki Prefecture in 1995, 1997 and 1999.

CPUE

Catch per unit effort (CPUE) is defined as catch per boat per day in this study. Annual CPUE in Iwate Prefecture increased remarkably from 1986 (1.9 tonnes) to 1990 (6.3 tonnes) (Fig. 2-6). It fluctuated between 4.6 and 7.0 tonnes from 1991 to 1995, but leveled off at 4.8-5.9 tonnes since 1996. Annual CPUE of bow-mounted trawls in Miyagi Prefecture was high (about 4 tonnes) in 1987, 1993, 1994, 2000 and 2001, but was low (about 2 tonnes) in 1990, 1991, 1995 and 1997. It was 0 or nearly 0 tonnes in 1996, 1998 and 1999. Annual CPUE of seine boats in Miyagi Prefecture was high in 1992 (7.8 tonnes) and 2000 (8.3 tonnes), but was low from 1996 to 1999, especially in 1996 (4.1 tonnes) and 1997 (5.1 tonnes). Annual CPUE of seine boats averaged 6.1 tonnes from 1991 to 2001, but annual CPUE of bow-mounted trawls averaged 2.7 tonnes during the same period in Miyagi Prefecture. Therefore, fishing efficiency of seine boats was suggested to be more than two times higher than that of bow-mounted trawls. Annual CPUE in Fukushima and Ibaraki prefectures showed the similar change, being higher than 4 tonnes in 1987, 1992-1994, 2000 and 2001, but about 2 tonnes in 1985, 1988 and 1990. Annual CPUE in 1995, 1997 and 1999 was 0 or nearly 0 tonnes in both prefectures, except for in 1995 in Fukushima Prefecture. Krill abundance in the Fukushima coastal waters in 1995 was perhaps low because the fishing period was very short (only 8 days), although annual CPUE was intermediate (3.2 tonnes).

Annual catch in Iwate and Miyagi prefectures has generally fulfilled the regulated catch since 1993, but annual catch in Fukushima and Ibaraki prefectures has been lower than the regulated catch since 1994 (Fig. 2-6). Total catch limit was set as the sum of bow-mounted trawls and seine boats in Miyagi Prefecture (Table 2-3) but the total catch substantially depended on the catch by seine boats since 1994 (Fig. 2-3). Therefore, it is suggested that the regulation on total catch limit did not strongly affect the annual CPUE of bow-mounted trawls in Miyagi Prefecture and seine boats in Fukushima and Ibaraki prefectures. Accordingly, these CPUEs are suggested to reflect the real abundance of krill resources. Annual CPUE of bow-mounted trawls in Miyagi Prefecture from 1984 to 2001 has a significant negative correlation ($P < 0.05$) with SFO during February and July but does not have a significant negative correlation with the lowest surface temperature in the Sanriku coastal waters (Fig. 2-7). Annual CPUE of seine boats in Ibaraki Prefecture from 1984 to 2001 has a significant negative correlation ($P < 0.05$) with both SFO during February and July and the lowest surface temperature in the Joban coastal waters (Fig. 2-7).

Fishing period

First fishing day was generally in early-or mid-February in the Sanriku coastal waters (Fig. 2-8). However, it should be noted that the limit of first fishing day in the Sanriku coastal waters has been regulated since 1993 (Table 2-3), so the first fishing day did not always reflect to the natural environmental conditions. On the other hand, the first fishing day has occurred after mid February, thus the regulation on the first fishing day (1 February; Table 2-3) had not been substantial in the Joban coastal waters (Fig. 2-8).

The first fishing day in the Joban coastal waters from 1984 to 2001 has a significant positive correlation ($P < 0.05$) with both SFO during February and July and the lowest surface temperature in the Joban coastal waters (Fig. 2-9). The first fishing day in the Joban coastal waters from 1984 to 2001 has a significant negative correlation ($P < 0.05$) with annual CPUE in Ibaraki Prefecture during the same period (Fig. 2-10).

The last fishing day was determined not only by the rising of temperatures concurrently with the northward shift of the warmer Kuroshio waters but also by social and economic reasons. For example, the sudden plunge of unit price of *E. pacifica* fishery triggered the conversion to the sand lance fishery in

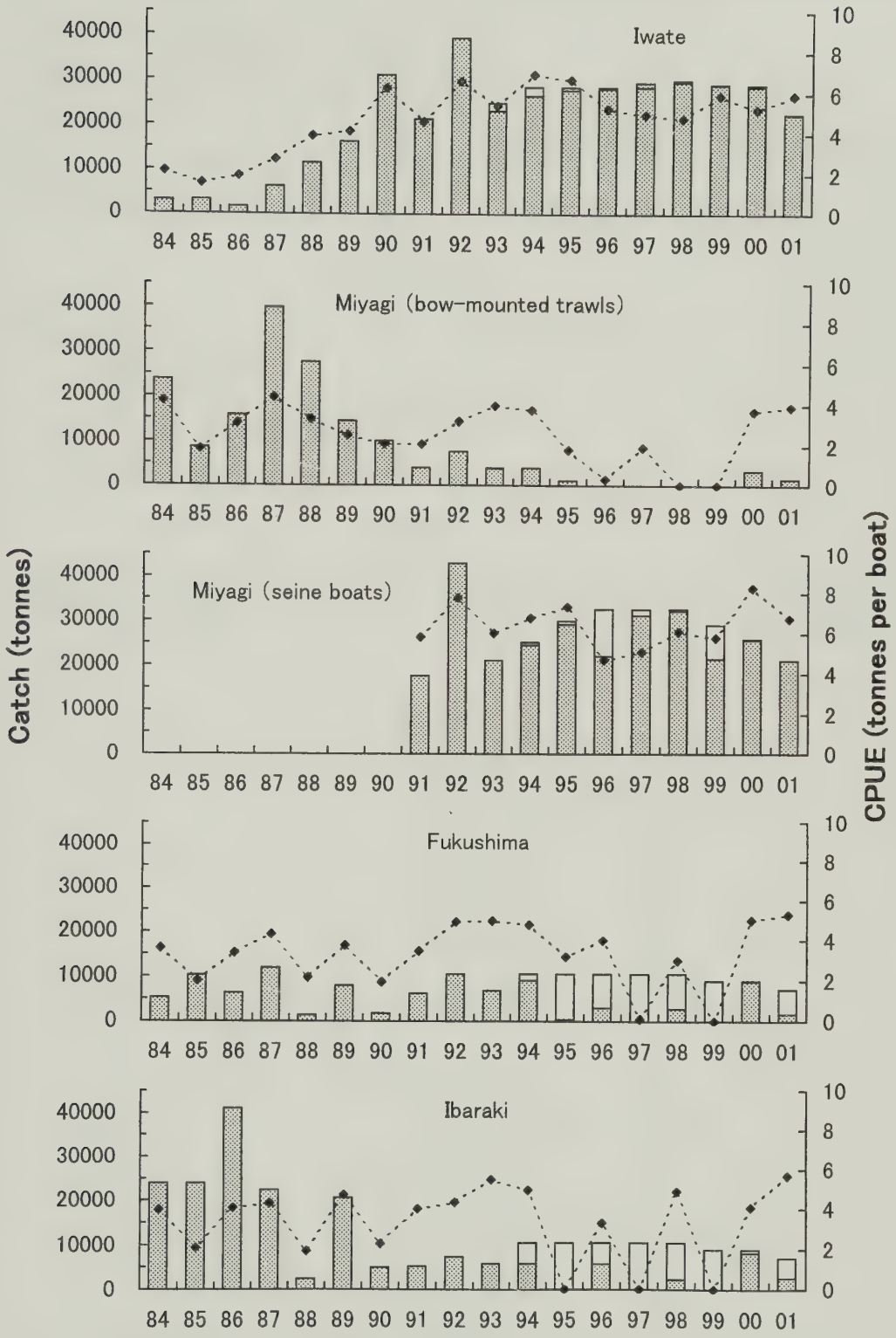

Fig. 2-6. Annual variations in the catch (dotted bars) and CPUE (line). Open bars represent the remainder of the total regulated catch after accounting for actual landings. The regulated value shown for seine boats in Miyagi Prefecture from 1994 to 2001 is calculated as the total regulated value over the prefecture value minus the actual catch of bow-mounted trawls fishing.

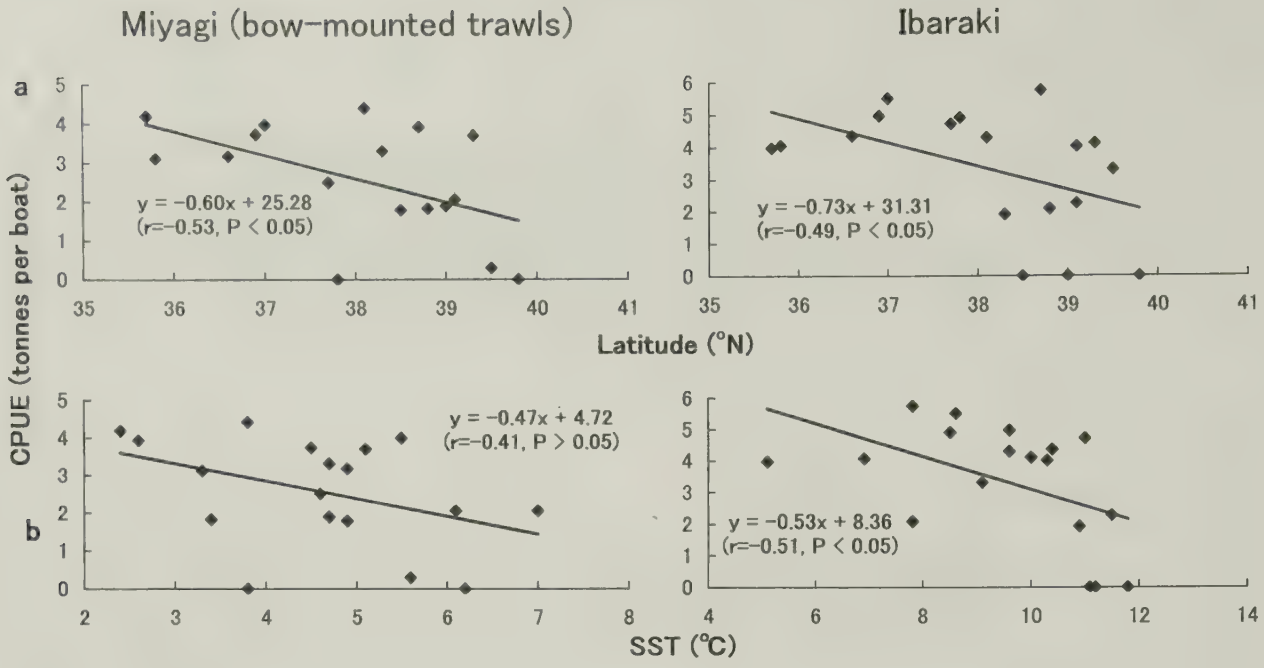

Fig. 2-7. Relationship between the annual CPUE in Miyagi (bow-mounted trawls) and Ibaraki prefectures and the southernmost latitude of the first branch of the Oyashio Current (SFO) during February and July (a), and between the CPUE and the lowest SST along the Sanriku and Joban coastal waters (b).

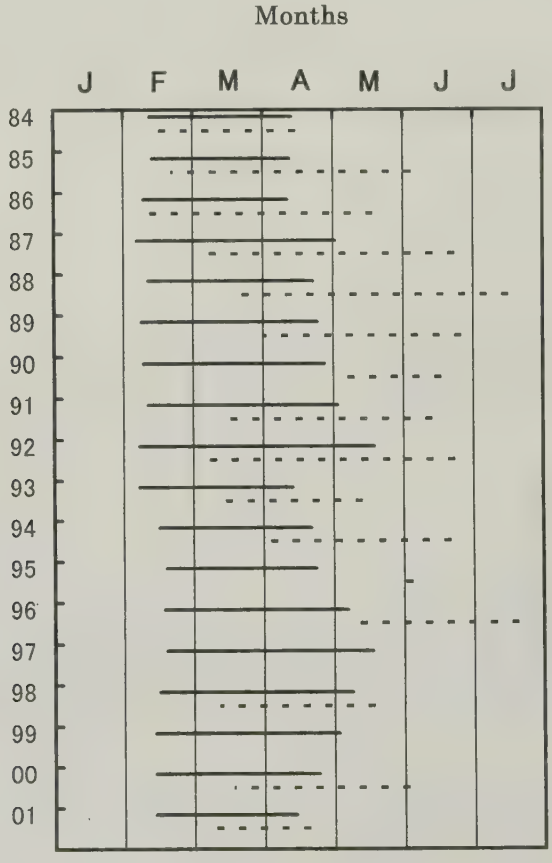

Fig. 2-8. Fishing period in Sanriku (solid lines) and Joban (broken lines) waters from 1984 to 2001. The first fishing day is defined as the first day when the catch was larger than 5 tonnes and fishing continued for the next 3 days. The last fishing is defined as the last day when the catch was larger than 5 tonnes and fishing had been conducted within the previous 3 days.

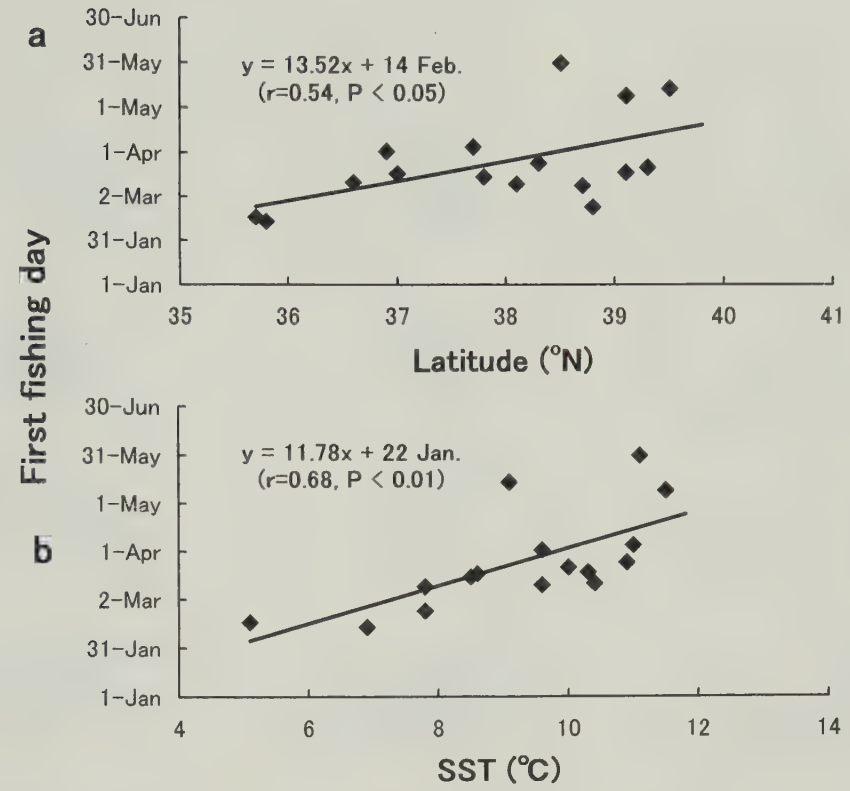

Fig. 2-9. Relationship between the first fishing days along Joban coastal waters and SFO during February and July (a) and between the first fishing days and the lowest SST along Joban coastal waters (b).

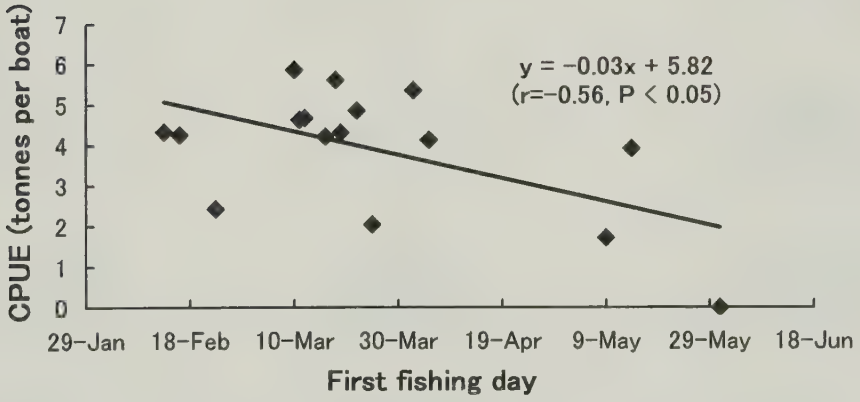

Fig. 2-10. Relationship between the first fishing day along Joban coastal waters and the annual CPUE of Ibaraki Prefecture.

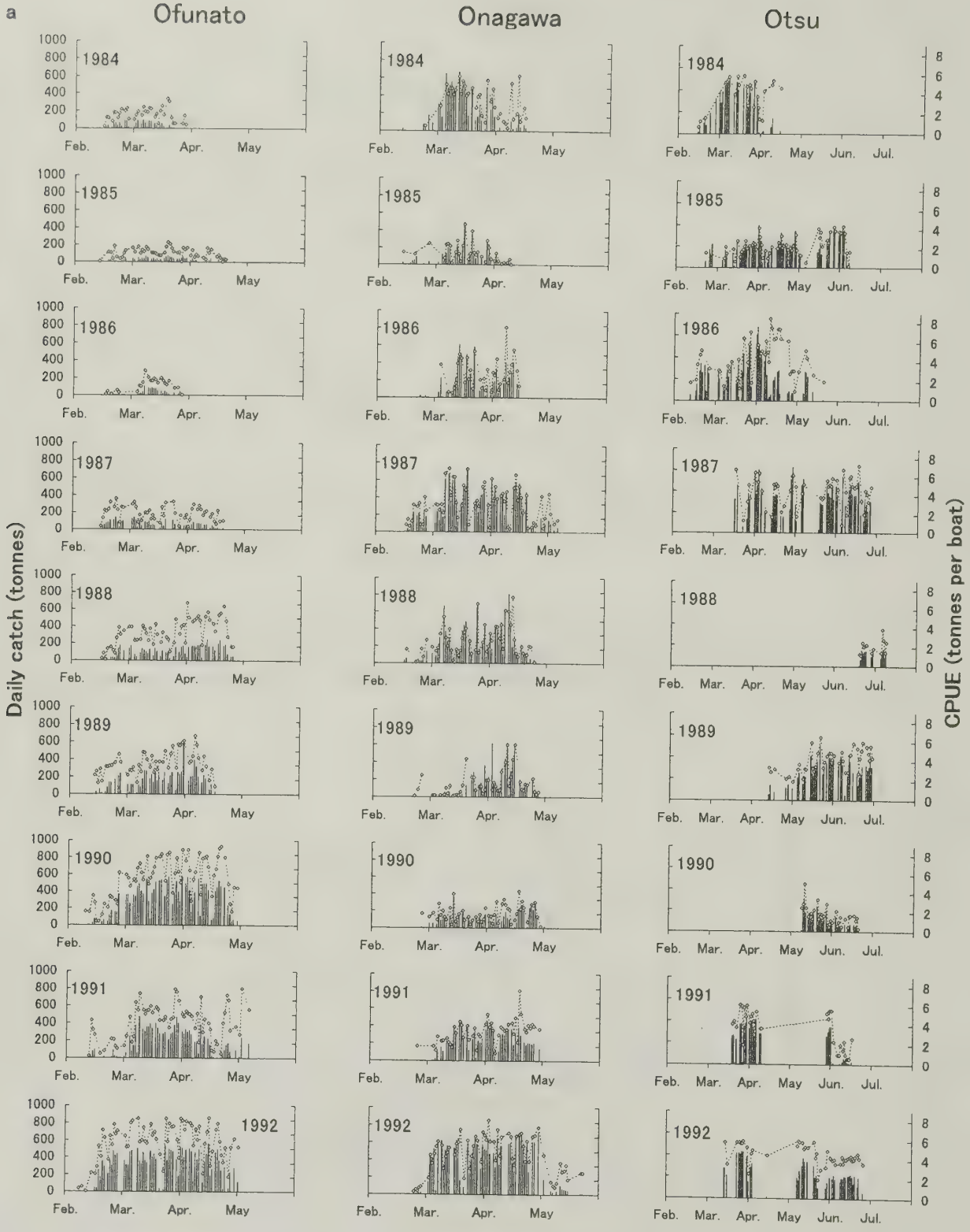

Fig. 2-11. Daily catch (bars) and CPUE (line) at the three principal ports; Ofunato (Iwate Pref.), Onagawa (Miyagi Pref.) and Otsu (Ibaraki Pref.). a: 1984-1992, b: 1993-2001.

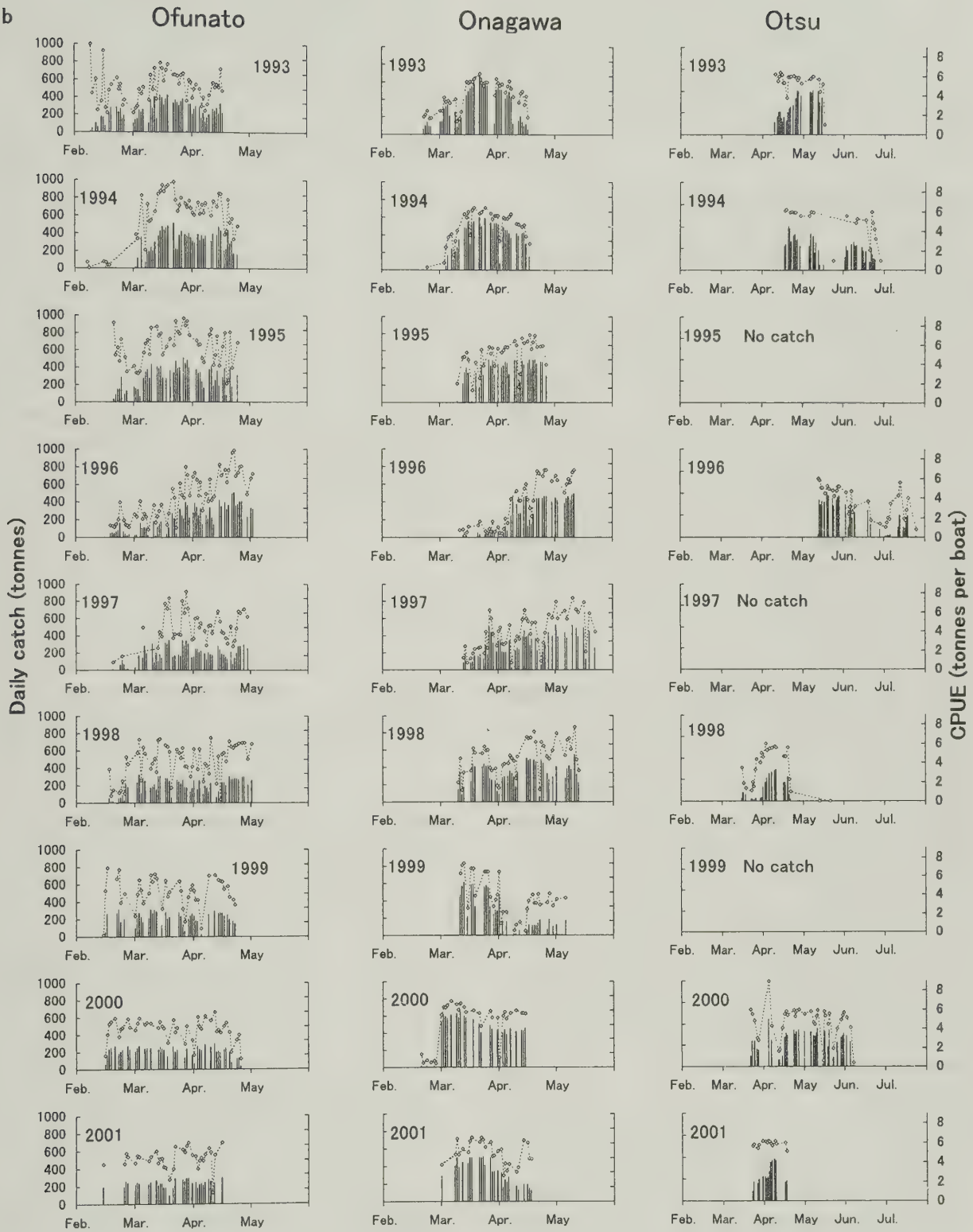

Fig. 2-11. Continued (1993-2001).

1984 and 1986 in the Joban coastal waters. On the other hand, the fishing had been generally finished due to fulfillment of the regulated catch since 1993 in Iwate and Miyagi prefectures. CPUE tended to remain high level in the last fishing day in Ofunato and Onagawa ports (Fig. 2-11).

Location of fishing ground from 1995 to 2001

The weekly change in location of fishing ground with surface temperature isotherms was examined from 1995 to 2001 as follows.

[1995] The fishing ground was formed in the coastal waters off the middle part of Iwate Prefecture, located on the coastal side of the 7℃ isotherm related to the first branch of the Oyashio Current, in late February (Fig. 2-12). It tended to shift southward with the southward shift of 7℃ isotherm from early March to late March. However, it was limitedly formed on the north side of Oshika Peninsula (ca. 38°20'N) and not formed on the warmer side than 10 ℃ isotherm from late March to late April.

[1996] The fishing ground was formed in the coastal waters off northern or middle part of Iwate Prefecture, located on the coastal side of the 7℃ isotherm related to the first branch of the Oyashio Current, during mid- and late February (Fig. 2-13). It expanded southward along the 7℃ isotherm to the upper continental slope off Oshika Peninsula from late March to late April. It was formed in the coastal waters off northern part of Ibaraki Prefecture near the 10℃ isotherm in mid-May. It was formed in the upper continental slope off Fukushima and Ibaraki prefectures near the 15℃ isotherm in mid June. The *E. pacifica* fishery in the Joban coastal waters lasted until late July in this year.

[1997] The fishing ground was formed in the coastal waters off the middle part of Iwate Prefecture, located on the coastal side of the 7℃ isotherm related to the first branch of the Oyashio Current, in mid-February (Fig. 2-14). It expanded southward along the 7℃ isotherm to the coastal waters off northern part of Miyagi Prefecture from early March to late March. However it was formed in the upper continental slope off Iwate and Miyagi prefectures near the 5-7℃ isotherms related to the second branch of the Oyashio Current which intruded southward instead of the northward retreat of the first branch of the Oyashio Current during mid- and late April. In mid-May, it was formed in the coastal waters off northern part of Miyagi Prefecture, located on the warmer side than 10℃ isotherm. In this year, the fishing ground had been rarely formed in the Joban coastal waters.

[1998] The fishing ground was formed in the coastal waters off Iwate Prefecture, located on the coastal side of 5℃ isotherm related to the first branch of the Oyashio Current, in mid-February (Fig. 2-15). It expanded southward along the 7℃ isotherm to the coastal waters off Ibaraki Prefecture from late February to late March. It was formed in the upper continental slope off Iwate and Miyagi prefectures near the 5-7℃ isotherms in early March and mid-April.

[1999] Warm-core ring cut off from the Kuroshio Extension occurred off Iwate Prefecture had been blocking the southward shift of the first branch of the Oyashio Current (Fig. 2-16). The fishing ground was formed in the upper continental slope off the middle part of Iwate Prefecture near the 7℃ isotherm related to the first branch of the Oyashio Current in mid-February, but it expanded southward to the coastal waters off northern Miyagi Prefecture along with the southward shift of the 7℃ isotherm from late February to late March. However, warm-core ring was close to the coastal waters off Iwate Prefecture and then the fishing ground was divided into two areas off northern Iwate Prefecture and northern Miyagi Prefecture in early April. The latter area located near the 7℃ isotherm related to the second branch of the Oyashio Current. The fishing ground had not been formed south of the Oshika Peninsula in this year.

[2000] The fishing ground was formed in the coastal waters off middle part of Iwate Prefecture, and was located on the southwest side of the 7℃ isotherm related to the first branch of the Oyashio Current, in mid-February (Fig. 2-17). It expanded southward along with the southward shift of the 7℃ isotherm to the coastal waters off northern part of Ibaraki

Prefecture from mid February to late March. Since then, it had been formed in the Joban coastal waters until mid-May. It was formed on the warmer side than 10℃ isotherm from late April to early May.

[2001] The fishing ground was formed in the coastal waters off the middle part of Iwate Prefecture in mid-February (Fig. 2-18). It shifted to the coastal waters off southern part of Iwate Prefecture and Miyagi Prefecture from late February to mid-March, when the 0℃ isotherm was close to the coastal waters off northern-middle Iwate Prefecture. However, it expanded from north to south of the coastal waters off Iwate Prefecture in early April, when the 5 ℃ isotherm was close to the coastal waters off middle part of Iwate Prefecture instead of the northward retreat of 0℃ isotherm. The fishing ground was formed in the coastal waters off the boundary area between Fukushima and Ibaraki prefectures near the 7℃ isotherm from mid-March to early April.

Discussion

Development of *Euphausia pacifica* fishery

The history of the *E. pacifica* fishery was classified into four time periods as follows.

During the first period (from the mid-1940s to the late 1960s), a small-scale fishery was conducted limitedly in the vicinity of the Oshika Peninsula in Miyagi Prefecture for local consumption and culture baits.

During the second period (from the late 1960s to the late 1980s), the fishing grounds were extended throughout the Sanriku and Joban waters and the annual total catch increased substantially, because strong demands for the fished *E. pacifica* for aquaculture and sport fishing increased remarkably, and fishing and storage techniques developed. The southward shift of SFO also contributed to expand fishing grounds into Joban during this period (Fig. 2-2).

During the third period (from the late 1980s to the early 1990s), the main fishing grounds shifted to the Sanriku coastal waters. This shift was thought to be triggered by the northward retreat of SFO during this period (Fig. 2-2). Especially, fishing efforts and catches increased concurrently with the establishment of the seine boat method in Iwate Prefecture. On the other hand, both fishing efforts and catches decreased in the Jonan coastal waters, and the unit price of landing in this waters has strongly depended on that in the Sanriku coastal waters since this period.

During the fourth period (from the early 1990s to 2001), annual and daily total catch has been regulated due to control the unit price of the fished *E. pacifica*. *E. pacifica* fishery has been exclusively conducted from February to April in the Sanriku coastal waters, nevertheless other fisheries such as seine boats for sand lance and squid jiggling are run together by the same vessels (Minato, pers. comm.). Iwate and Miyagi prefectures have dominated the *E. pacifica* fishery and maintaining the stable unit price (approximately 40 yen per kg) by setting several regulations. The *E. pacifica* fishery in the Joban coastal waters has been easily replaced by other fisheries such as sand lance and Shirasu (larval Japanese anchovy) when fishing condition of *E. pacifica* is not favorable in the Joban coastal waters. The fishing ground of Shirasu is formed when the Kuroshio warmer waters prevailed. The unit price of Shirasu is much higher than that of *E. pacifica* and the workload onboard of Shirasu fishery is lighter than that of *E. pacifica* fishery (Ando, pers. comm.).

It is suggested that the regime shift in the Pacific Ocean had occurred in the mid-1970 and late 1980 (Minobe, 1997; Yasunaka and Hanawa, 2002). Watanabe *et al.* (2003) suggested that the strength in southward shift of the Oyashio Current is closely related to the decadal change of the Pacific Ocean. Annual catch of *E. pacifica* increased mainly along the coastal waters off Miyagi Prefecture and Joban from mid-1970 to 1987, but increased mainly along the coastal waters off Iwate Prefecture instead of decrease in Joban after 1988. Therefore, the history of *E. pacifica* fishery has been closely related to the regime shift in the Pacific Ocean. Kodama *et al.* (1995) showed that colder fish species such as walleye pollack, Pacific cod, herring and sand lance increased from mid-1970 to 1987 but decreased after 1988 with the shift of oceanographic condition in the vicinity of Kinkazan Island. Abundant *E. pacifica* transported by the first branch of the Oyashio Current may af-

Fig. 2-12. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1995 off northeastern Japan. Iw: Iwate ; Mi: Miyagi; Fu: Fukushima; Ib: Ibaraki. Figures indicate SST (℃). Modified from 'Quick reports on fishing and oceanographic conditions' from Japan Fisheries Information Service Center.

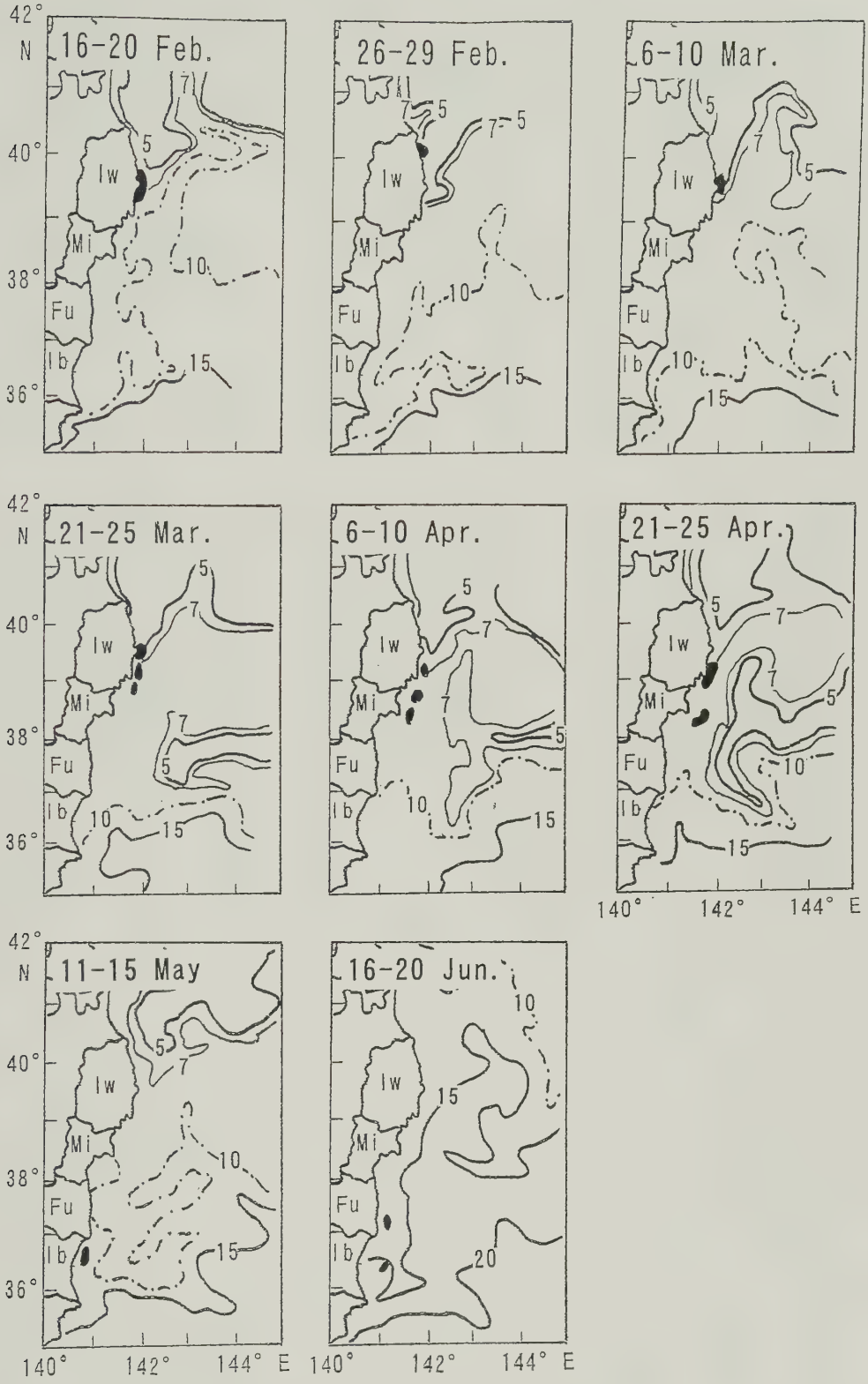

Fig. 2-13. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1996 off northeastern Japan. Details are as shown in Fig. 2-12.

Fig. 2-14. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1997 off northeastern Japan. Details are as shown in Fig. 2-12.

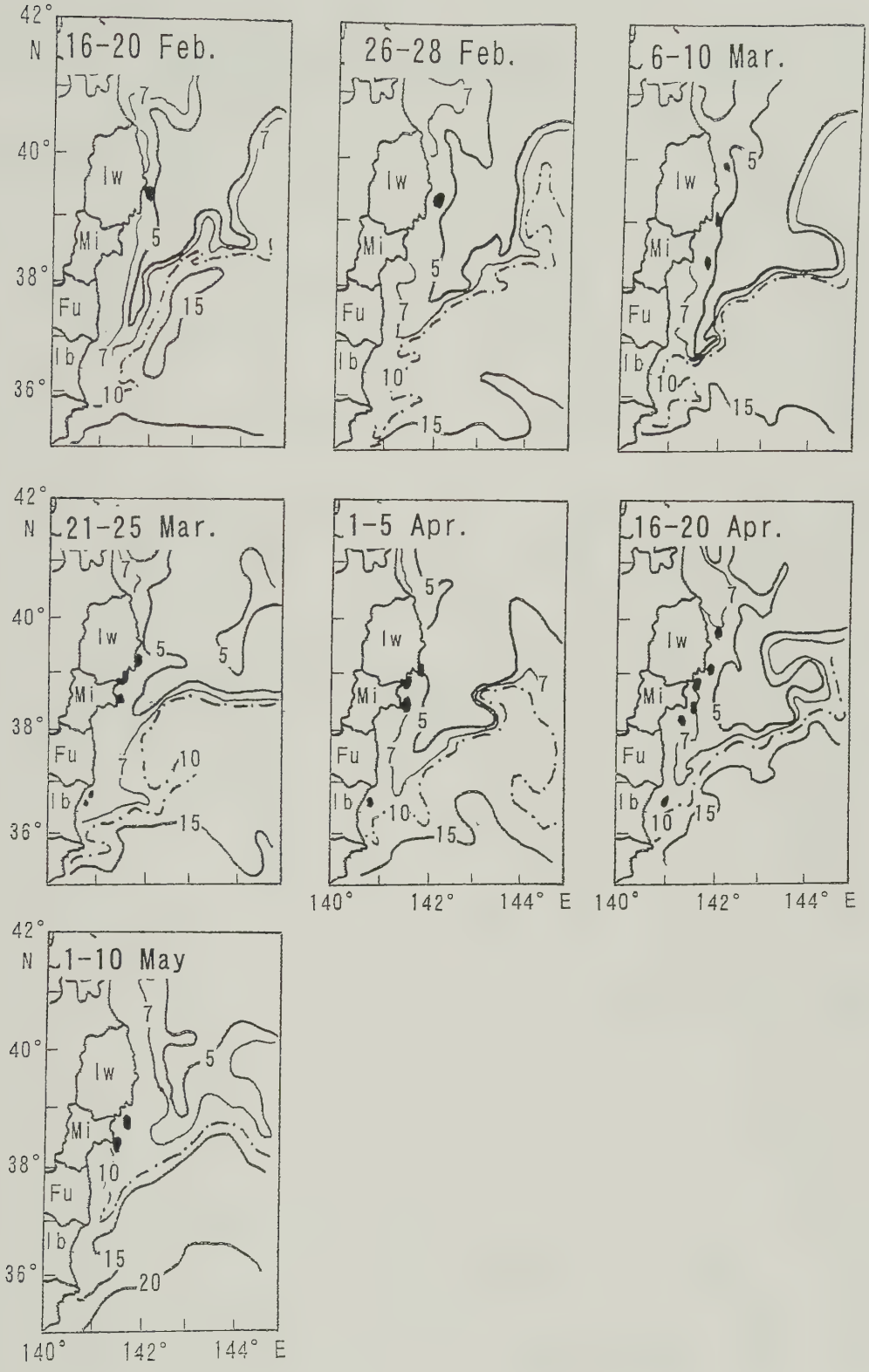

Fig. 2-15. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1998 off northeastern Japan. Details are as shown in Fig. 2-12.

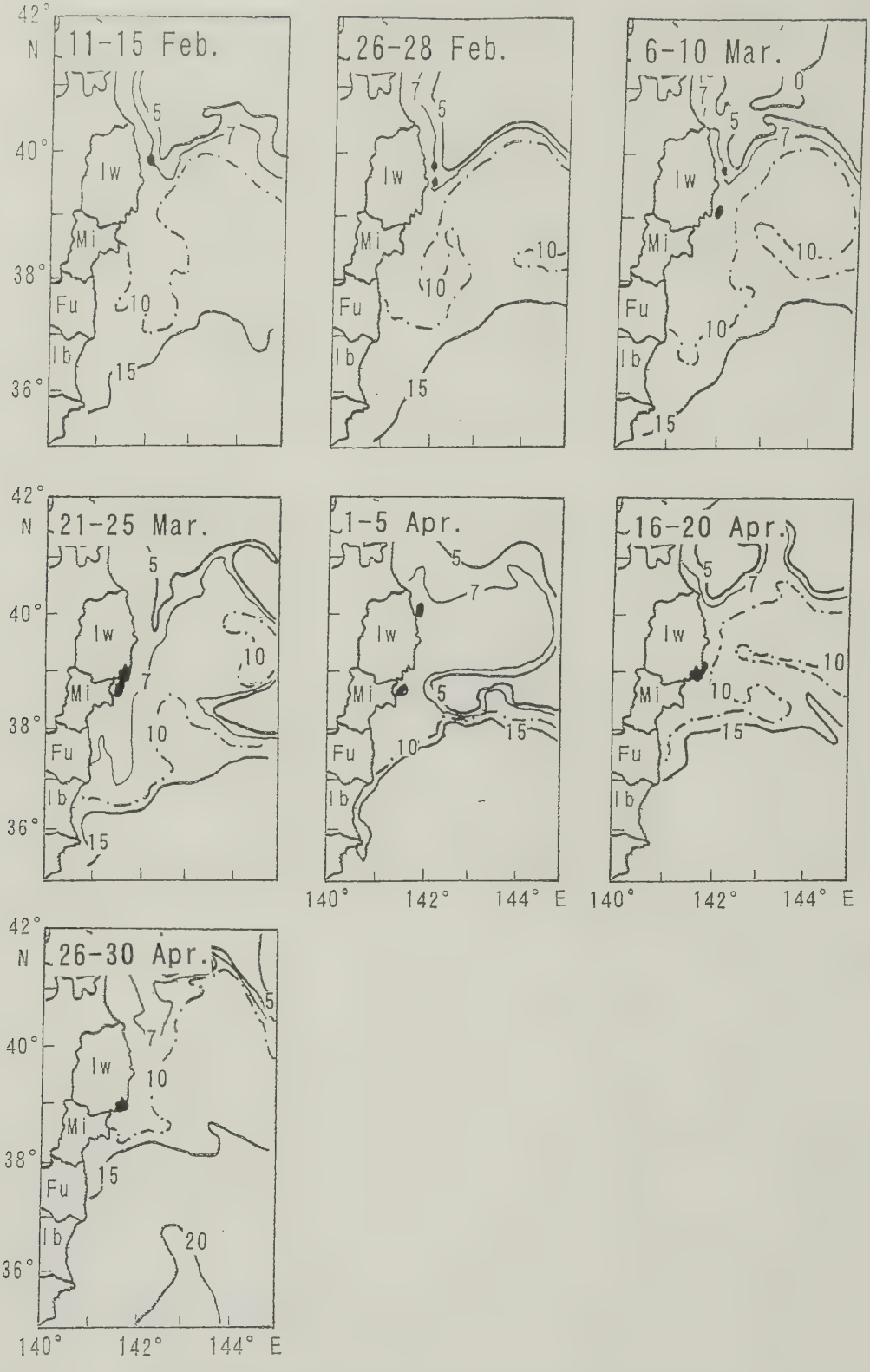

Fig. 2-16. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 1999 off northeastern Japan. Details are as shown in Fig. 2-12.

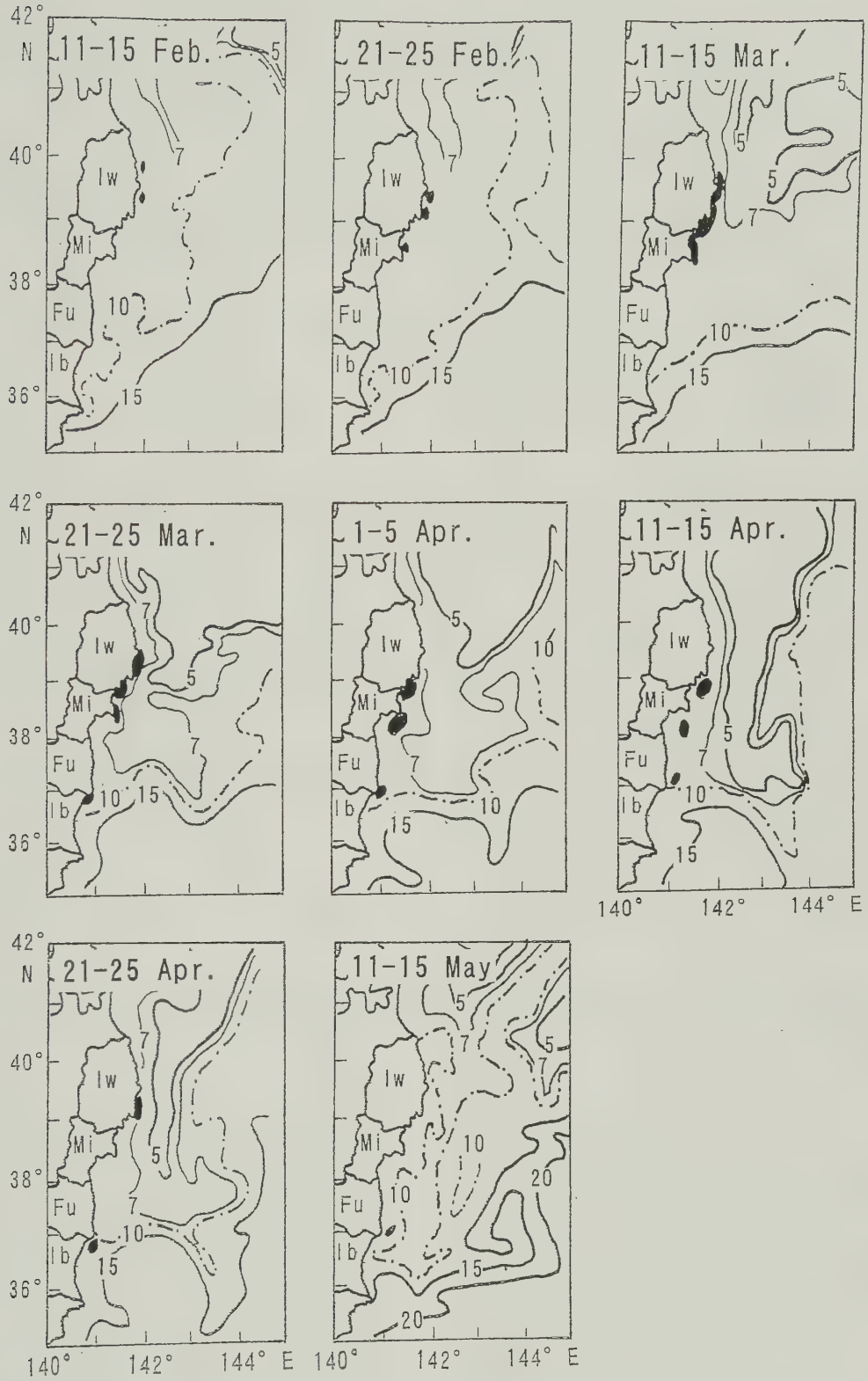

Fig. 2-17. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 2000 off northeastern Japan. Details are as shown in Fig. 2-12.

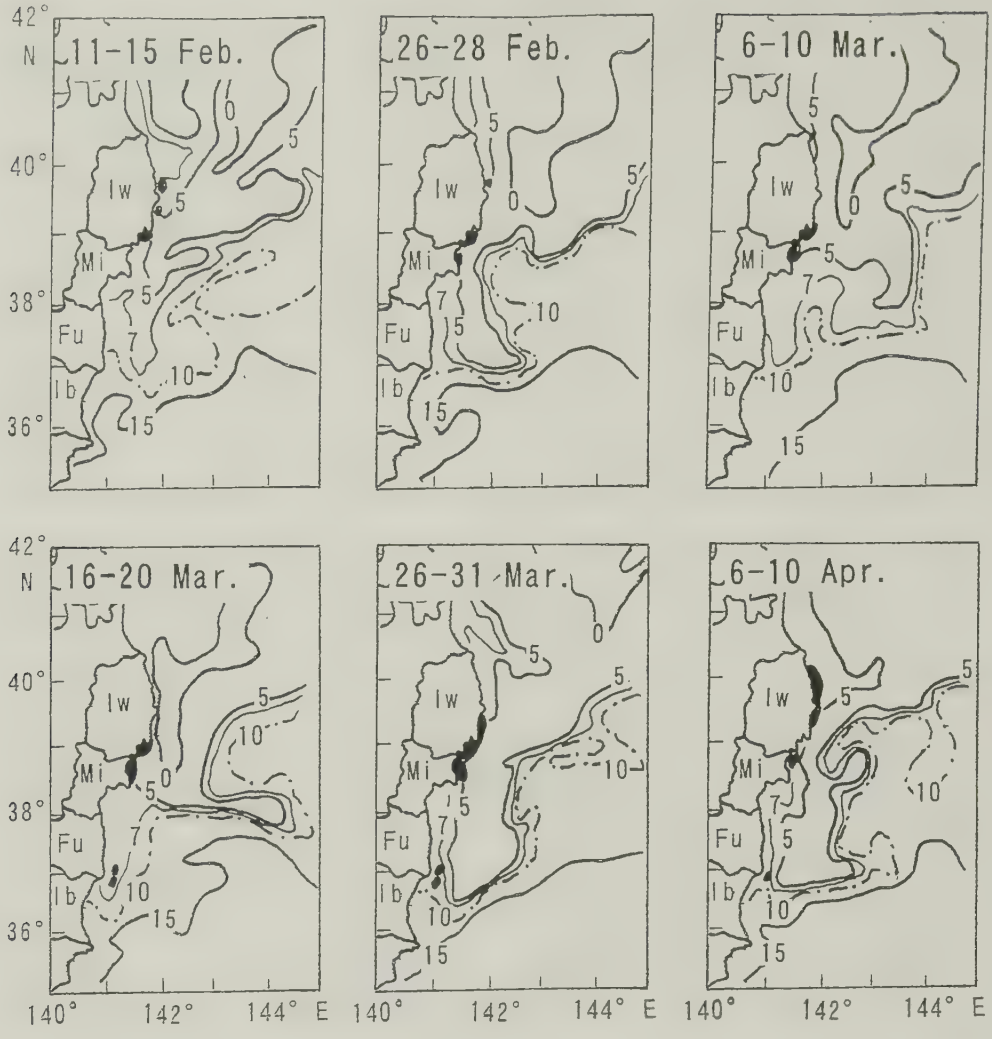

Fig. 2-18. Locations of *Euphausia pacifica* fishing grounds (black area) in relation to sea-surface temperatures in 2001 off northeastern Japan. Details are as shown in Fig. 2-12.

fect the good condition for growth and reproduction of these fishes in the colder years.

Relationship between oceanographic conditions and fishing conditions

Several studies have examined the mechanisms of formation of fishing grounds since 1960s (Komaki, 1967; Endo, 1981; Odate, 1991; Kodama, 1995a). Kodama (1995a) classified oceanographic patterns in the vicinity of Kinkazan Island, Miyagi Prefecture into three types based on the *E. pacifica* fishing conditions as follows. (1) When the Oyashio Current is moderately strong narrowing the area with suitable temperatures (5-7℃) in the Sanriku coastal waters, *E. pacifica* is concentrated there and good catches are expected. (2) When the Oyashio Current is weak and only present in the northern part of Sanriku waters, poor catches are expected. (3) When the Oyashio Current is very strong and comes close to the shore, suitable temperatures are restricted to the Joban area, a larger catch is landed in the Joban area compared to the Sanriku area.

Annual CPUE of the bow-mounted trawls in Miyagi Prefecture has a significant negative correlation with SFO during February and July, which is consistent well with Kodama's (1) and (2) pattern (Fig.

2-7). On the other hand, the fishing conditions of seine boats in Miyagi Prefecture are difficult to examine because total catch limits has been set since 1993. However, annual CPUE was significantly low from 1996 to 1999 when SFO during February and July showed the northward shift except in 1998 (Fig. 2-2). Therefore, it is suggested that fishing conditions are generally unfavorable when the Oyashio Current is weak in Miyagi Prefecture.

The catch of bow-mounted trawls in Miyagi Prefecture was low but the catch in Joban coastal waters was high in 1977 and 1981 when SFO during February and July showed a large southward shift (Figs. 2-2 and 5). Odate (1991) suggested that most of the target populations in these years migrated toward the Joban coastal waters according to the strong southward current of the first branch as Kodama's (3) pattern. Both Odate (1991) and Kodama (1995a) suggested that the water <5℃ is not suitable for *E. pacifica*. Because the fishing ground was formed off southern Iwate Prefecture when the 0℃ isotherm was close to the coastal waters off northern-middle Iwate Prefecture during late February and mid-March 2001 (Fig. 2-18), it is suggested that *E. pacifica* avoids at least such extreme cold temperatures.

The remarkable increase of catch and CPUE in Iwate Prefecture was mainly due to the increase in number of seine boats and active introduction of hydro-acoustic. The reason why annual CPUE after 1996 was slightly lower than that before 1996 was partly due to the strengthening of the regulation on the total landing limits per boat for the purpose of the maintenance of appropriate unit prices against the increase of fishing vessels in 1996 and 1997 in Iwate Prefecture (Minato, pers. comm.). Therefore, it is difficult to examine how oceanographic condition affects the fishing condition in this Prefecture. However, annual CPUE did not decrease when SFO was northward anomaly. Thus, the reason why the fishing condition in Iwate Prefecture was rather stable is suggested to be due to regular occurrence of suitable temperatures (5-7℃) for *E. pacifica* near the coastal waters off Iwate Prefecture in spring even in the northward anomaly years (Figs. 2-13, 14 and 16).

Annual CPUE in Ibaraki Prefecture has a significant negative correlation with SFO during February and July and the lowest temperature in the Joban coastal waters (Fig. 2-7). The first fishing day in the Joban coastal waters has significant positive correlation with both SFO during February and July and the lowest temperature in the Joban coastal waters (Fig. 2-9). Thus the fishing conditions in the Joban coastal waters are thought to be affected significantly by the southward shift of the first branch of the Oyashio Current and surface colder waters.

The relationship between fishing conditions and oceanographic conditions is concluded as follows. When the first branch of the Oyashio Current is weak, fishing condition in Iwate Prefecture is rather stable but not in Miyagi Prefecture and Joban, showing low CPUE and delayed formation of fishing ground. On the other hand, when the first branch of the Oyashio Current is strong, fishing condition in Miyagi Prefecture and Joban area is favorable as well as in Iwate Prefecture, showing high CPUE and early formation of fishing ground.

When comparing these results there are two key points that need to be born in mind. The first is that only catch per boat per day is used as the relative abundance density (CPUE) and the absolute density of each target population can not be analyzed in this approach. Therefore, the fishery data on catch per tow and towing time for each boat should be collected together to elucidate a more appropriate abundance index and to allow comparison of the density of swarms between different fishing grounds in the future. The second point is that the fishing grounds gradually extended to the area with the high thermal isotherms after May up to 15℃ isotherm in June (Figs. 2-13, 14 and 17), although they were usually formed along the 5-7℃ isotherms at the surface and their southward distributional limits rarely reached at 10℃ isotherm during February and April. This phenomenon is thought to be related to the seasonal change of vertical distribution pattern of *E. pacifica* and of physical condition in the mid-layer off Joban as discussed in the Chapter 7 'General discussion'.

Chapter 3. Distribution and life history of *Euphausia pacifica*

Given the wide distributional range of *Euphau-*

sia pacifica as well as probable horizontal advection, large areas need to be surveyed using the same gear and methods to effectively investigate the life history of this species. To date, however, population dynamics studies of *E. pacifica* in the northwestern Pacific have been conducted at a few fixed stations (Endo, 1981; Terazaki *et al.*, 1986).

In this chapter, seasonal changes in spawning, distribution and growth pattern and life span of *E. pacifica* off northeastern Japan were investigated using Norpac net samples collected widely (mainly 36°-43°00' N and west of 145°E) from several monthly multi-vessel line transect surveys during 10 years, and the average pictures of the distribution and life history of *E. pacifica* off northeastern Japan were examined. In addition, seasonal changes in spawning and distribution of *E. pacifica* in several fixed stations from off southeastern Hokkaido to Joban (36°50'-42°50'N) were investigated bimonthly using cylindrical-conical nets with large mouth opening, and geographical changes of spawning and distribution of *E. pacifica* were examined in relation to water masses.

Materials and Methods

Norpac net survey

A total of 3,073 discrete Norpac net samples was collected during 206 cruises in the northwestern Pacific between the years 1992 and 2001 (Table 3-1). These collections were from 13 oceanographic and fishery research institutions conducting monthly multi-vessel line transect surveys to examine oceanographic conditions or Pacific saury and squid resources. The sampling area was between 35°30'-48°00'N and west of 158°E, however about 70% of the Norpac net samples were carried out between 36°-43°00' N and west of 145°E (Fig. 3-1). Nets (mouth opening 45 cm and mesh opening throughout 335 μm; no closing mechanism) were lowered to 150m depth, and hauled vertically to the surface at 1 m s^{-1} while the vessel was stationary for all stations. Samples were preserved in 5% buffered formalin seawater immediately after collection.

E. pacifica were sorted into its developmental stages except for the nauplius and metanauplius stages, most of which would pass through nets. Although the identification of euphausiid eggs is difficult, *E. pacifica* type eggs were classified as having a capsule diameter of 0.4-0.5mm and embryo diameter of 0.30-0.38mm based on the size of eggs in Sanriku waters in April 1992, when *E. pacifica* dominated (Taki and Kotani, 1994). The length for the post-calyptopis stages was measured from the tip of the rostrum to the distal end of the telson to the nearest 0.1mm. Adults were sexed according to the presence of a thelycum in females or petasmas in males. Mature male euphausiids have one pair of ejaculatory ducts on the ventral side of cephalothorax which contains developed spermatophores, and males attach the spermatophores to the thelycum of females during mating. However, no female *E. pacifica* specimens were observed with more than two spermatophores in this study. So, it is thought that a male *E. pacifica* attaches its spermatophore to the thelycum during mating, and the female with a spermatophore avoids mating until it casts with the exuviae the spermatophore at the subsequent moult. Evidence of mating, i.e. the presence or absence of a spermatophore (hereafter as copulated females) was checked for females. The abundance of each developmental stage and each 1 mm length class was calculated on the assumption that the filtering rate was 100% for all samples. Only night samples were used for the calculation of average abundance (1,406 hauls) and length measurements (1,151 hauls) of post-calyptopis stages, because they migrate below 150 m depth in daytime, but mostly are at <150 m depth at night (see Chapter 4).

Water masses were classified on the basis of the temperature at 100m depth as the Oyashio area (OW; ≦5℃), cold waters of the transitional area (CW; >5℃, ≦10℃), warm waters of the transitional area (WW; >10℃, ≦15℃), and Kuroshio area (KW; >15℃), based on the water mass classifications of Odate (1994) and Yokouchi *et al.* (1997).

Average surface temperature was highest in August-September, and lowest in February-April (January in KW), when water mixing between the surface and deeper layer actively occurs in each water mass (Fig. 3-2). The order of higher temperature was KW > WW > CW > OW in every month.

Growth and age structure were analyzed from length-frequency distributions, using a comput-

er program devised by Tsutsumi and Tanaka (1988), which is modified from the graphic methods of Cassie (1954) and Taylor (1965).

Cylindrical-conical net survey

Seven surveys were carried out using Norpac nets and 5.5-m long cylindrical-conical nets (net mouth diameter: 1.3m; mesh size: 0.45mm; Watanabe, 1992) on the R. V. *Wakataka-maru* (Tohoku National Fisheries Research Institute, Fisheries Research Agency), *Tankai-maru* and *Hokko-maru* (Hokkaido National Fisheries Research Institute, Fisheries Research Agency) from March 1997 to February 1998. To compare the ecological parameters of *E. pacifica* between geographic areas, the survey area was divided into three areas: 1) off southeastern Hokkaido, 2) Sanriku and 3) Joban (Fig. 3-3). Two or three transects were set for each coastal area, and a zigzag line between 100 and 300m isobaths off Sanriku and Joban was added in March and April in order to conduct an acoustic survey (Miyashita *et al.*, 1998). Off Sanriku and Joban, the survey stations were set at about 100, 200, 300, 500 and 1,000 m isobaths. Off southeastern Hokkaido, the stations were set at about 100, 200, 300, 500, 1,500 and 1,700m isobaths. Note that the March survey was carried out only off Sanriku, and three offshore stations near the marginal area of the first branch of the Oyashio Current were added in August.

Norpac nets were vertically towed above 150m at 1 $m s^{-1}$. At the stations where the bottom depth was shallower than 150m, Norpac net was towed from the near bottom to the surface. Cylindrical-conical nets were obliquely towed at 2 knots of the ship speed from 15m above the sea bottom to the surface at the stations where the sea depth was shallower than 300m, and towed from 150m to the surface in other stations. A wireless net recorder (CN-24: FURUNO) was attached on the bridle 2.5m ahead of the mouth of the cylindrical-conical net to monitor the net depth at the bridge. Cylindrical-conical net was towed only at night at all stations because post-calyptopis stages migrate below the 150m depth in the daytime, but mostly occur at $<$ 150m depth at night (see Chapter IV), except at stations along the zigzag acoustic lines in March and April. A flowmeter (Rigosha) was mounted in the mouth of both nets to register the volume of water passed through the net. Samples were preserved with 5% formalin seawater immediately after collection. Water temperature and salinity from 0 to 300m depth were measured by CTD (Sea-Bird), and water samples were collected from 0, 10, 30, 50, 75m depth to determine chlorophyll *a* concentrations at all stations in March and April, at stations along the southeast line from 42° 50'N, 144° 50'E, and at stations along the east lines from 40° N, 38° 20'N and 36° 50'N.

E. pacifica were sorted and classified into developmental stages except for the nauplius and metanauplius stages, most of which would pass through both nets. The abundance of eggs and calyptopis stage was determined from the Norpac net collections, those of furcilia, immature and adult stages from the cylindrical-conical net collections. Identification of developmental stages, sex and reproductive condition and measurements of body length for post calyptopis stages were conducted according to the same methods as done in the Norpac net survey.

Results

Seasonal changes in the developmental stage composition in water masses

In OW, copulated females and eggs showed high abundances in April and May, and showed another peak during August-October (Fig. 3-4). Calyptopis, furcilia and immature stages were most abundant in May, and these stages showed a second peak during August-December. Copulated females and pre-adult stages rarely occurred in January and February. Seasonal changes in abundance of small ($\leqq$15mm) and large ($>$15mm) adults were more stable than those of the pre-adult stages, but both showed higher abundance during August-October.

In CW, copulated females and eggs showed the highest abundance in April, and showed a second small peak during August-November (Fig. 3-4). In April, eggs in this water mass were remarkably more abundant than in the other water masses. Calyptopis, furcilia and immature stages were most abundant in May, and those stages showed a second peak during August-December in OW. The abundances of calyptopis and furcilia stages in this water mass were comparable to their abundances in OW in

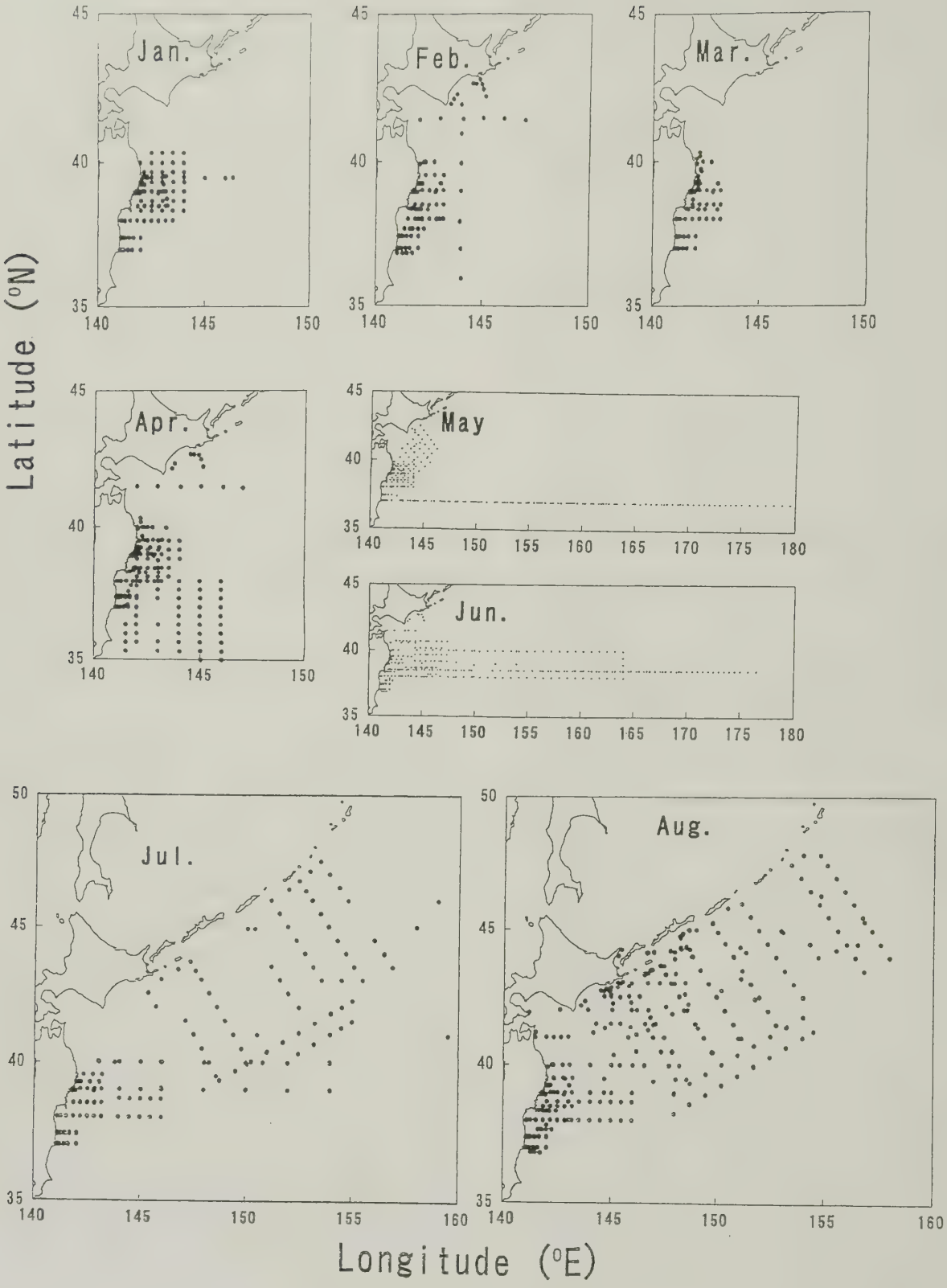

Fig. 3-1. Sampling locations of zooplankton using Norpac net in the northwestern Pacific for each month from 1992 to 2001.

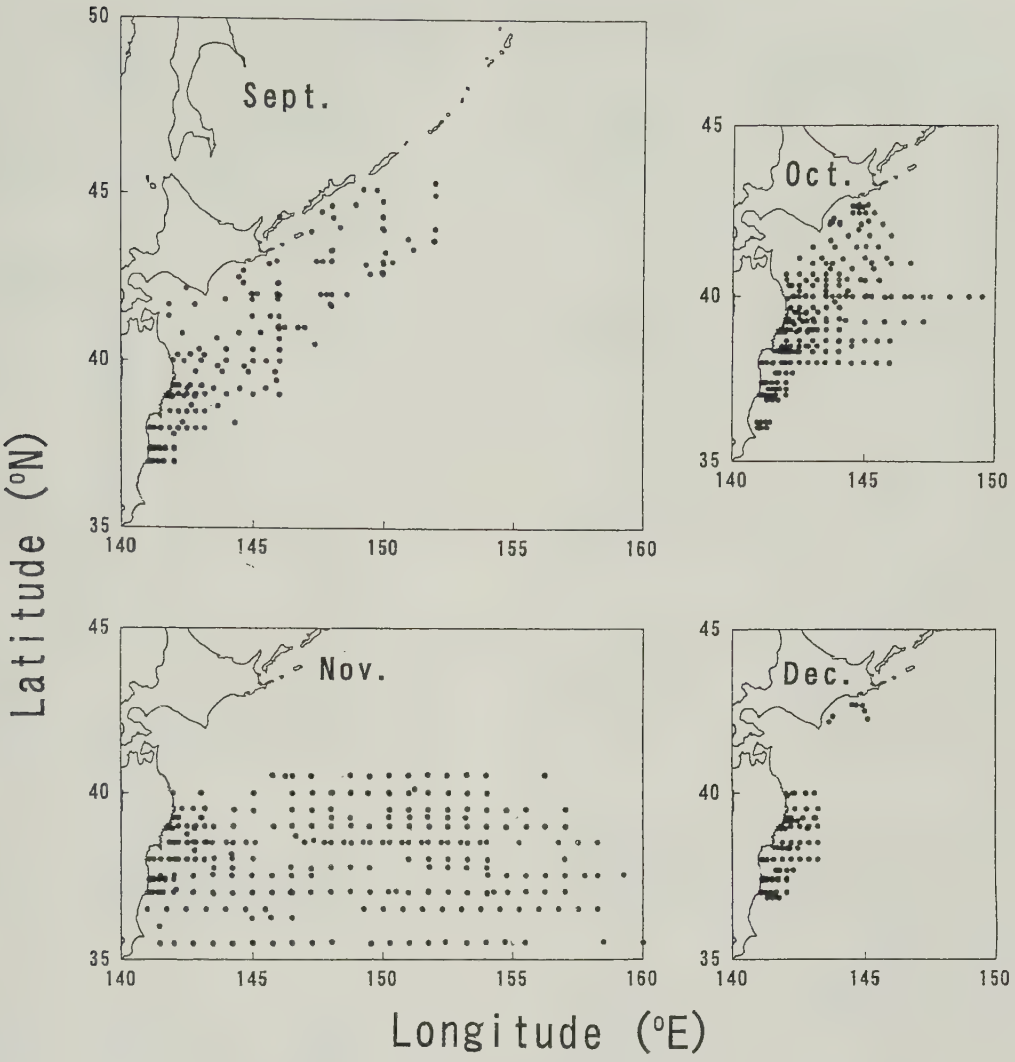

Fig. 3-1. Continued.

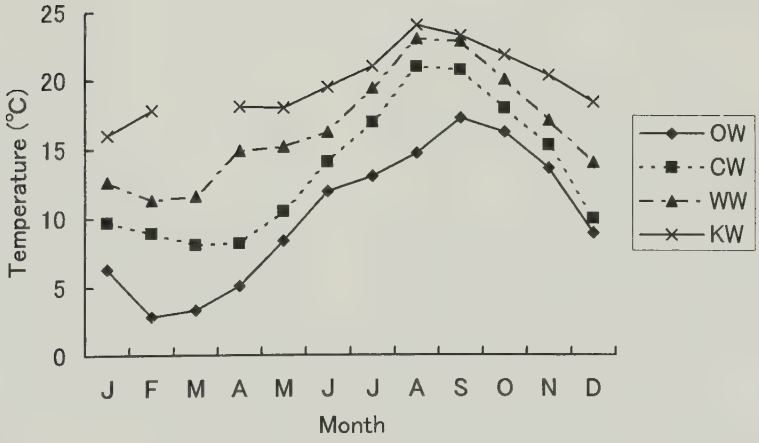

Fig. 3-2. Seasonal changes in the average surface temperature in OW, CW, WW and KW.

Table 3-1. Number of Norpac net samples per month during 1992-2001

month	area	number of samples			years	month	area	number of samples			years
		Day	Night[*1]	Total				Day	Night	Total	
	OW[*2]	2	3 (0)	5	'95,'96		OW	53	30 (29)	83	'93～'99
	CW[*3]	37	42 (32)	79	'94～'00		CW	54	23 (15)	77	'93～'99
Jan.	WW[*4]	32	33 (28)	65	'94～'00	Jul.	WW	59	34 (18)	93	'93～'95
	KW[*5]	0	2 (1)	2	'97		KW	0	1 (1)	1	'98
	Total	71	80 (61)	151			Total	166	88 (63)	254	
	OW	14	15 (13)	29	'94,'96,'98		OW	143	117 (117)	260	'93～'99
	CW	33	27 (16)	60	'94,'96～'00		CW	61	46 (38)	107	'93～'99
Feb.	WW	12	14 (12)	26	'94,'96～'99	Aug.	WW	85	36 (29)	121	'93～'99
	KW	0	1 (1)	1	'94		KW	7	6 (6)	13	'93,'94,'96'98
	Total	59	57 (42)	116			Total	296	205 (190)	501	
	OW	6	12 (10)	18	'94,'97,'98		OW	20	61 (61)	81	'93～'99
	CW	44	25 (12)	69	'94,'96～'99		CW	28	31 (20)	59	'93～'99
Mar.	WW	6	9 (8)	15	'94,'96～'99	Sept.	WW	68	29 (20)	97	'93～'99
	KW	0	0	0			KW	6	7 (7)	13	'93,'94,'96～'98
	Total	56	46 (30)	102			Total	122	128 (108)	250	
	OW	34	45 (41)	79	'93～'99		OW	21	30 (28)	51	'94～'00
	CW	50	59 (46)	109	'93～'99		CW	36	46 (29)	82	'93～'00
Apr.	WW	6	15 (12)	21	'95～'97,'99	Oct.	WW	63	88 (72)	151	'93～'00
	KW	1	13 (13)	14	'96,'97		KW	6	11 (8)	17	'94.'95,'97,'99
	Total	91	132 (112)	223			Total	126	175 (137)	301	
	OW	35	23 (21)	58	'93～'95,'97～'99,'01		OW	8	14 (12)	22	'93～'96
	CW	82	44 (31)	126	'93～'99,'01		CW	9	18 (13)	27	'93～'97
May	WW	74	30 (25)	104	'93～'95,'98,'99,'01	Nov.	WW	55	70 (57)	125	'93～'98
	KW	21	6 (6)	27	'93,'94,'99,'01		KW	85	93 (93)	178	'93～'98
	Total	212	103 (83)	315			Total	157	195 (175)	352	
	OW	35	23 (20)	58	'93～'98		OW	0	4 (4)	4	'97
	CW	109	51 (36)	160	'93～'98		CW	1	12 (11)	13	'95,'97
Jun.	WW	118	29 (19)	147	'93～'98	Dec.	WW	20	38 (21)	58	'93～'98
	KW	4	3 (3)	7	'93～'95		KW	11	7 (6)	18	'94.'96～'98
	Total	266	106 (78)	372			Total	32	61 (42)	93	

[*1]Night data in perentheses indicate samples for which body length, sex and presence of a spermatophore were examined.
[*2]Oyashio waters
[*3]Colder waters of transitionl area
[*4]Warmer waters of transitional area
[*5]Kuroshio waters

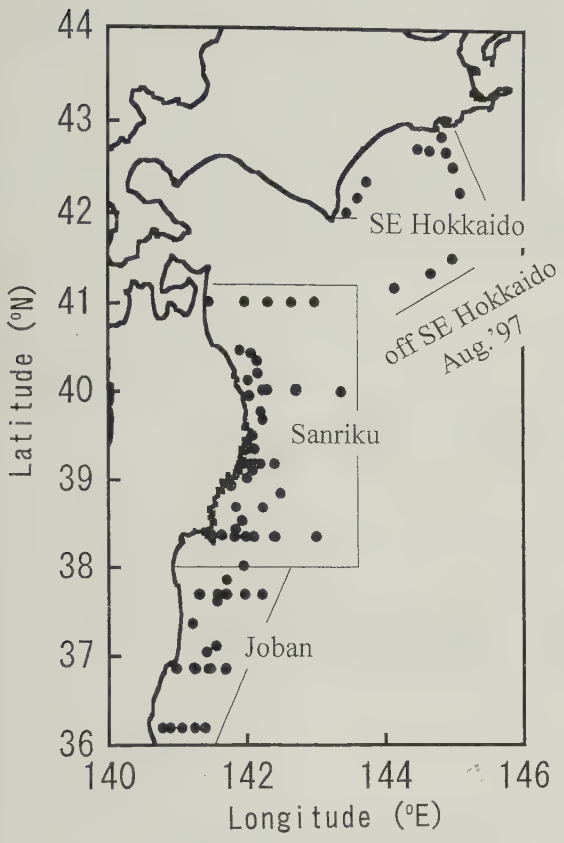

Fig. 3-3. Sampling locations of *Euphausia pacifica* off the northeastern coast of Japan from March 1997 to February 1998.

May. Copulated females and pre-adult stages rarely occurred in January and February as also observed in OW. Seasonal changes in abundance of small and large adults were more stable than those of pre-adult stages, but large adults rarely occurred in January and February. Both size adults in CW tended to be less abundant than those in OW throughout the year, but large adults in CW were more abundant than those in OW during March-June.

In WW, all stages of *E. pacifica* were less abundant than in the colder water masses except for large adults in July, when high abundance occurred at one station (Fig. 3-4). Seasonal variations of each stage were similar to those of CW, although the peak of calyptopis was observed a month earlier than in CW.

All of the stages rarely occurred in KW throughout the year (Fig. 3-4).

The average abundances of eggs, calyptopis and furcilia in CW were significantly higher (*t*-test, $P < 0.01$) than those in the other areas throughout the year (Table 3-2). The abundances of copulated females and immature stage in OW were as high as those in CW, and significantly higher (*t*-test, $P < 0.01$) than those in WW and KW. The abundances of small and large adults in OW were significantly higher (*t*-test, $P<0.001$) than those in the other areas, and the occurrence of large adults was mostly limited to OW and CW. This suggests that *E. pacifica* gradually adapts to colder areas with the developmental stage from furcilia to adults, and advanced-age adults rarely occur in warmer areas.

In OW and CW, copulated females mainly occurred in the 16-21mm size classes and the relative percentage of copulated females to the total abundance of females was 67-100% for >20mm size classes in April and May (Fig. 3-5). Copulated females mainly occurred > 16mm size classes in June, August and September. However, they also occurred among small size classes of 11-14mm from April to November.

Seasonal growth pattern and life span

In the monthly average length-frequency distributions in OW and CW, two modal size groups were generally recognized for male *E. pacifica*: both small and large adults occurred throughout the year (Fig. 3-6). It was difficult to rationally divide the size groups in April based only on the length-frequency data alone. By considering the sequence of modal groups from March to May, the groups were divided into three modal groups based.

Also two modal size groups were generally recognized for female *E. pacifica* in the monthly average length-frequency distributions in OW and CW, except for April, August and September when three groups were recognized (Fig. 3-7). Although it was difficult to rationally divide the modal size groups into two and three groups in March and April, respectively, these were considered to be composed of two and three groups, on account of the sequence of modal groups from February to May.

Based on the modal growth pattern, the average growth of males follows this pattern: The newly-appearing cohort of ca. 10mm in April shows slow, steady growth until the following March, but grows rapidly to ca. 17mm from March to June (Fig. 3-8).

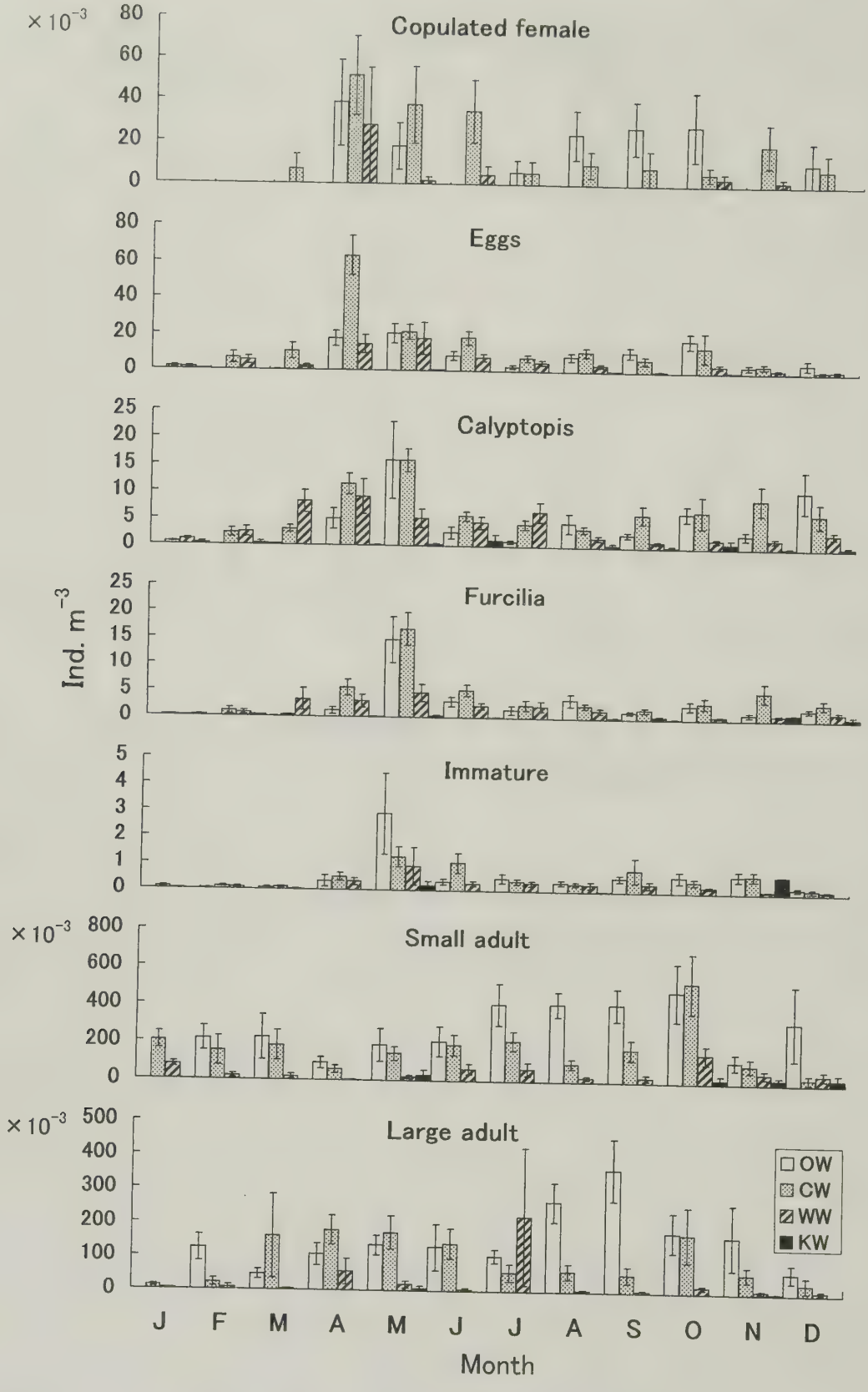

Fig. 3-4. Seasonal changes in the average abundance of each developmental stage of *Euphausia pacifica* by water mass from the Norpac net samples. Vertical bars: SE. No data from OW in January and KW in March. Details of theNorpac net samples are shown in Table 3-1.

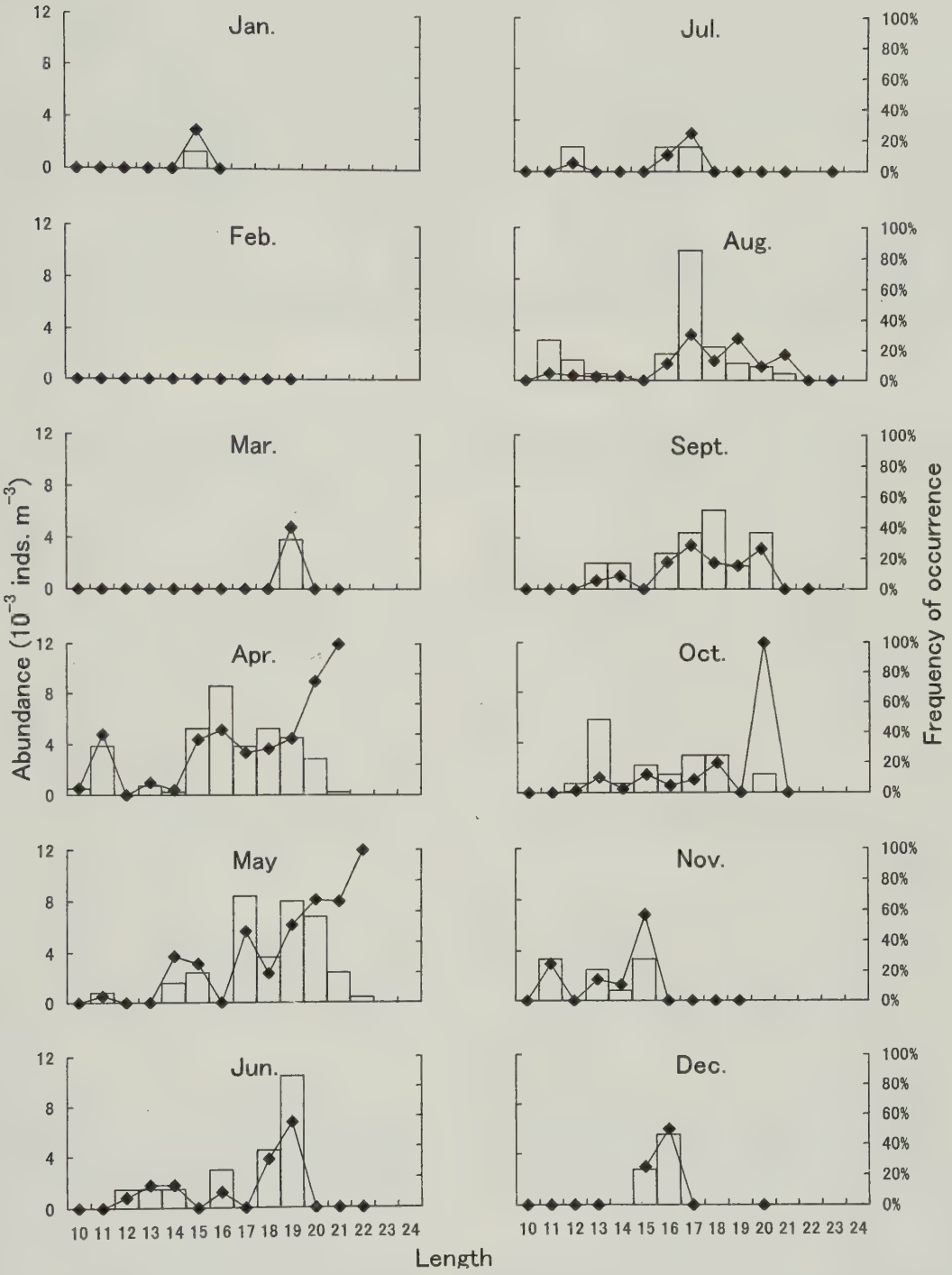

Fig. 3-5. Length-frequency distribution for *Euphausia pacifica* females with a spermatophore (bars) and their frequency (%) to the total abundance of females (solid diamonds) in OW and CW from the 10-year Norpac net samples.

Table 3-2. Average abundance (± SE; 10^{-3} inds. m^{-3}) of each developmental stage of *Euphausia pacifica* by water mass from the 10 year Norpac net samples*

stage / area	average abundance (±SE; 10^{-3} inds. m^{-3}) OW	CW	WW	KW
Copulated female	21±5.2 (48)	20±4.1 (46)	2.6±1.3 (6)	0
Eggs	9,700±1,100 (30)	17,700±1,800 (54)	5,200±1,000 (16)	235±56 (0.7)
Calyptopis	4,430±880 (31)	6,660±510 (46)	3,090±320 (21)	279±76 (1.9)
Furcilia	2,910±490 (33)	4,420±490 (50)	1,440±180 (16)	128±58 (1.4)
Immature	540±110 (40)	536±76 (40)	238±54 (18)	34±11 (2.5)
Small adult	328±32 (56)	173±21 (29)	67±12 (11)	20±9.8 (3.4)
Large adult	213±26 (62)	105±15 (31)	24±12 (6.9)	2.0±1.3 (0.6)

*Data in parentheses indicate percentage of abundance to the total for each developmental stage.

This cohort then seems to grow negatively after the summer to fall and attains a maximum of ca. 19mm by the following April. The seasonal growth pattern of females is similar to that of males except that the cohort of larger individuals (ca. 18mm) in April grew to ca. 20mm by August and existed until September (Fig. 3-8). Average length of males tended to be larger than that of females in winter but vice versa for the cohort of ca. 17mm during spring and fall.

Seasonal change in developmental stage composition among areas

Throughout the study period, the average temperatures at the surface and 100m depth off Joban were highest and those off southeastern Hokkaido were lowest (Fig. 3-9). The surface temperature was lowest in April or next February and highest in August-October along each coastal area. The temperature at 100m depth was lowest in April or next February and highest in October-December along each coastal area. Integrated average chlorophyll *a* concentration from 0 to 75m was highest in April and lowest in October along each coastal area.

The first branch of the Oyashio Current, characterized by a lower temperature than 5℃ at 100m depth (Murakami, 1994), extended southward to the Sanriku coastal area in March 1997, but it receded and another ≦5℃ water related to the second branch of the Oyashio Current occurred off Sanriku and Joban in April and June (Figs. 3-10-16). Oyashio waters (T_{100}≦5℃) gradually receded toward southeastern Hokkaido from August to December, but the first branch of the Oyashio Current strongly extended southward to Joban in the next February. Extreme cold temperatures < 2℃ occurred off southeastern Hokkaido during April and August. During the study period, the seasonal pattern of oceanographic conditions closely approximated the average seasonal pattern of this region (Ogawa, 1989).

Copulated females, eggs and calyptopis stage were abundant off Sanriku and Joban in April and off southeastern Hokkaido in October (Figs. 3-10, 11, 12 and 17). Both areas were near margins of the Oyashio waters (T_{100} = 5℃). Off southeastern Hokkaido, however, these abundances were low or non-existent throughout the year except in October, where cold waters of the Oyashio (T_{100} < 2℃) dominated. Eggs were present in June, but larvae were not observed in June and August. Therefore, spawning in June might not contribute to the recruitment to larvae off southeastern Hokkaido. Copulated females, eggs and calyptopis stage were also rare or absent off Sanriku and Joban from August to December, when warmer transitional waters (10℃ < T_{100}≦15℃) dominated. They were present only at the offshore stations near the margins of the first branch of the Oyashio Current in August. Their abundance was also very low throughout the survey area in December. In the following February, eggs and calyptopis stage were abundant off southern Sanriku and Joban, where colder transitional waters (5℃ < T_{100} ≦10℃) dominated. Seasonal change in the proportion of copulated females to total females was similar to that in abundance of copulated females and eggs (Fig. 3-17).

Distributional patterns of furcilia stage were similar to that of the younger stages (Figs. 3-13 and 17).

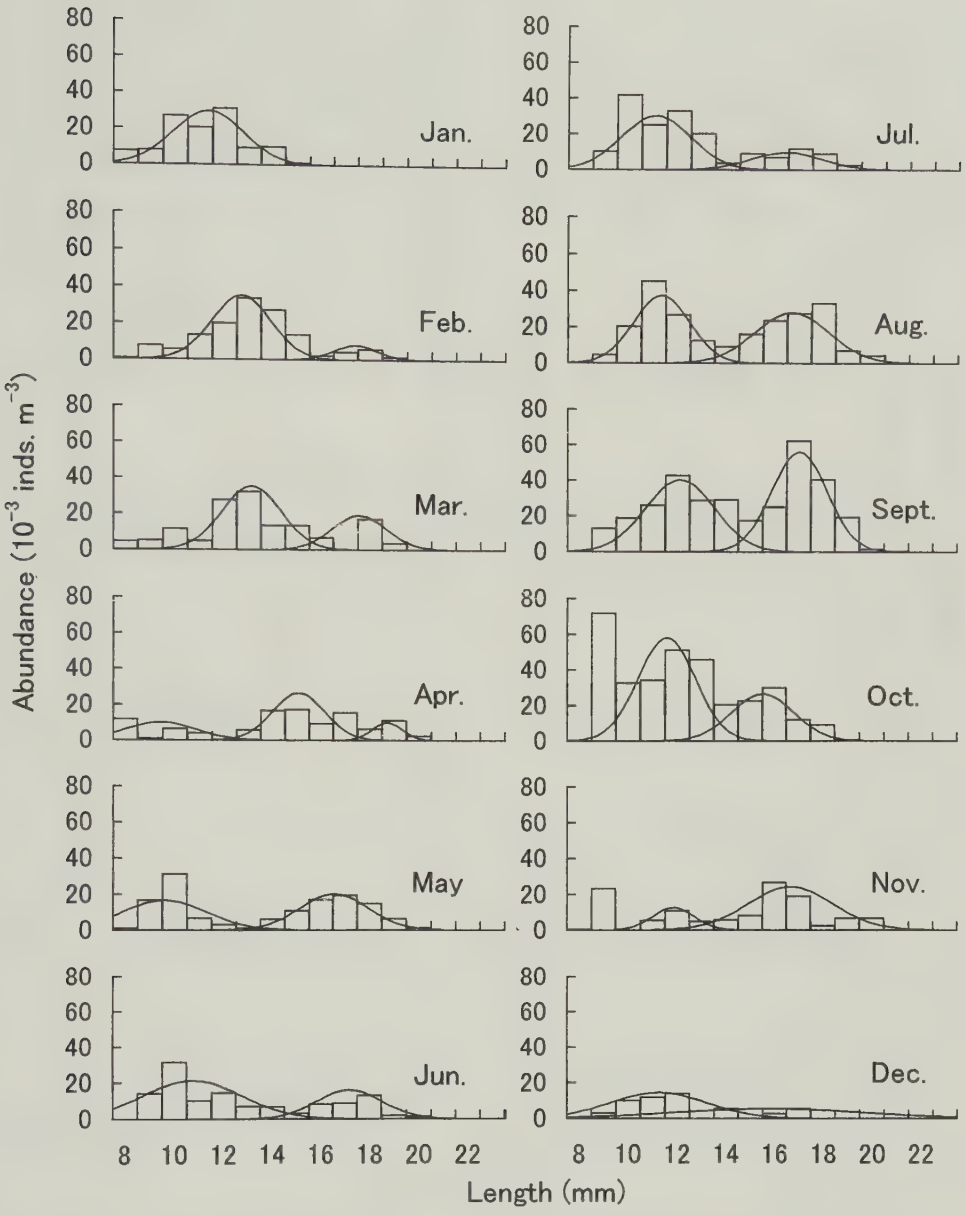

Fig. 3-6. Length-frequency distributions of male *Euphausia pacifica* in OW and CW from the Norpac net samples. Hypothetical distribution curve of each cohort is superimposed using a computer program devised by Tsutsumi & Tanaka (1988).

However, furcilia stage was rare off Sanriku and Joban in April, but abundant off Sanriku in December, where 10℃ isotherm at 100m depth occurred.

Immature stage was abundant off Sanriku and Joban from June to December and off southeastern Hokkaido in October, where temperatures at 100m depth were mainly between the 5 and 10℃ (Figs. 3-14 and 7). Immature stage tended to expand its distribution toward southern warmer areas as opposed to the younger stages. Immature stage was less abundant throughout the rest of the year than October off southeastern Hokkaido, although this stage was always present there.

Small adults occurred in all survey areas throughout the year. They were abundant in the survey area, especially off Sanriku in February, when the first branch of the Oyashio Current strongly moved southward (Figs. 3-15 and 17).

Large adults were abundant off Sanriku in March, April and the following February, while off Joban

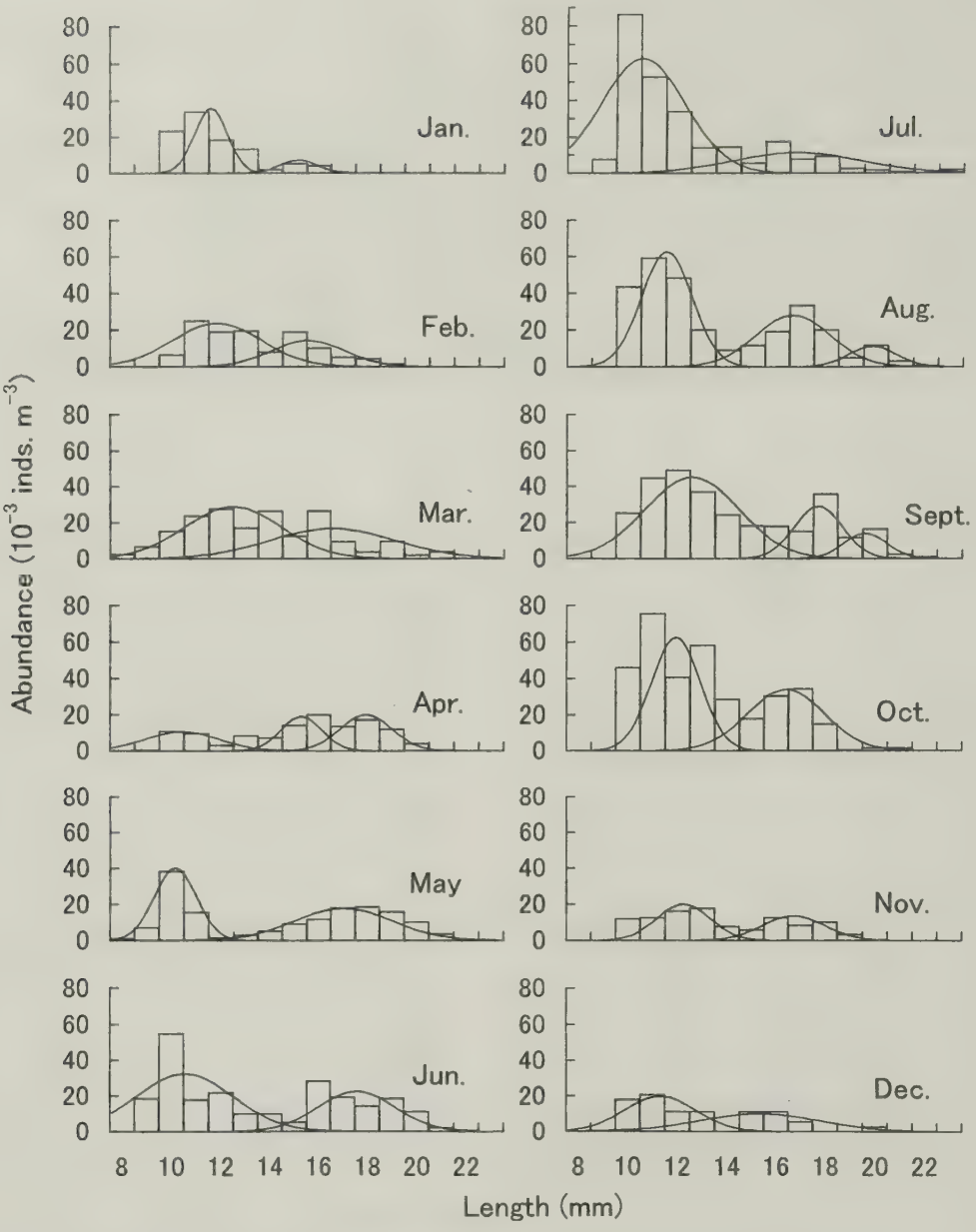

Fig. 3-7. Length-frequency distributions of female *Euphausia pacifica* in OW and CW from the Norpac net samples. Hypothetical distribution curve of each cohort is superimposed using a computer program devised by Tsutsumi & Tanaka (1988).

they were abundant in June and the following February. During these months, the 5℃ isotherm shifted southward. Large adults were few from August to December, when the warmer transitional waters dominated (Figs. 3-16 and 17). Off southeastern Hokkaido, they were not abundant in April, but increased after April and peaked in abundance in October. In December, they were rare throughout the survey area.

In April, copulated females mainly occurred among 17-21mm and 16-18mm size classes off Sanriku and Joban, respectively (Fig. 3-18). In June, they mainly occurred among 16-22mm size classes off Joban. In August, they mainly occurred among 11-12mm and 15-18mm size classes near the margins of the first branch of the Oyashio Current. In October, they mainly occurred among 12-14mm and 16-19mm size classes off southeastern Hokkaido. In February, they occurred across a wide size range of 10-19mm and mainly occurred among 16-18mm size

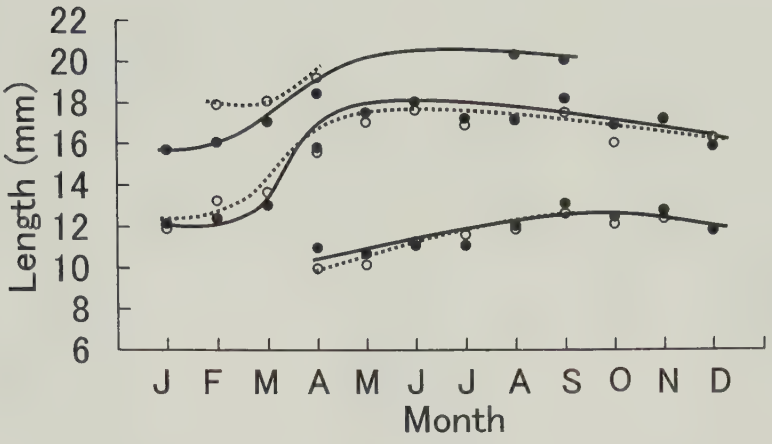

Fig. 3-8. Seasonal changes in the average length of each cohort of male (open circles) and female (solid circles) *Euphausia pacifica* estimated by the length-frequency distributions in OW and CW (Figs. 3-6 and 7). Lines: Hypothetical growth (males: dashed lines; females: solid lines).

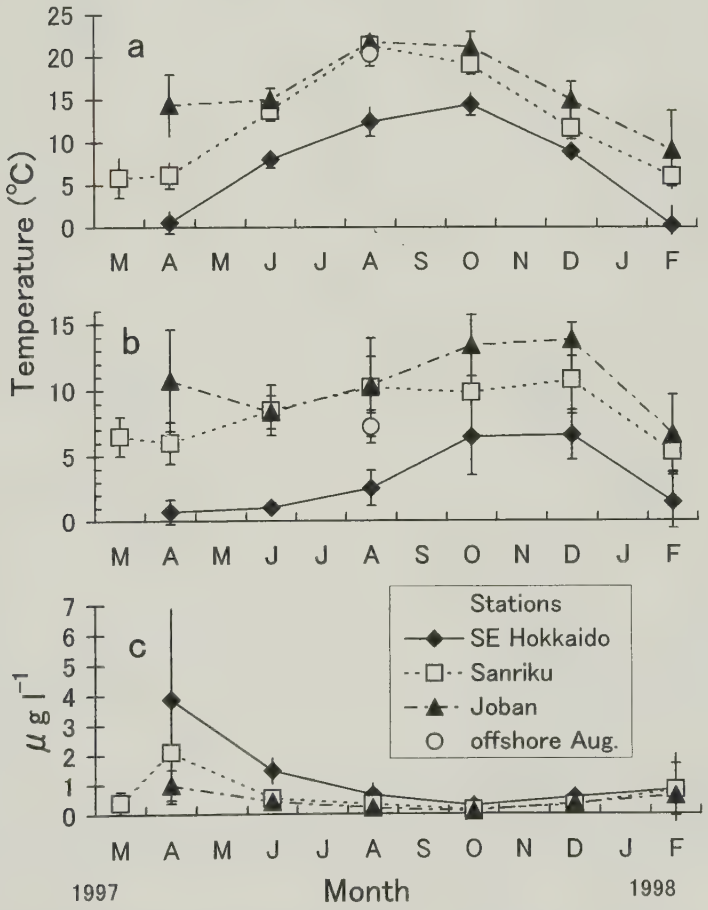

Fig. 3-9. Seasonal changes in the average surface temperature (a), average temperature at 100m depth (b) and integrated average chlorophyll *a* (μg l^{-1}) in the upper 75m (c). Vertical bars: ±1 SD.

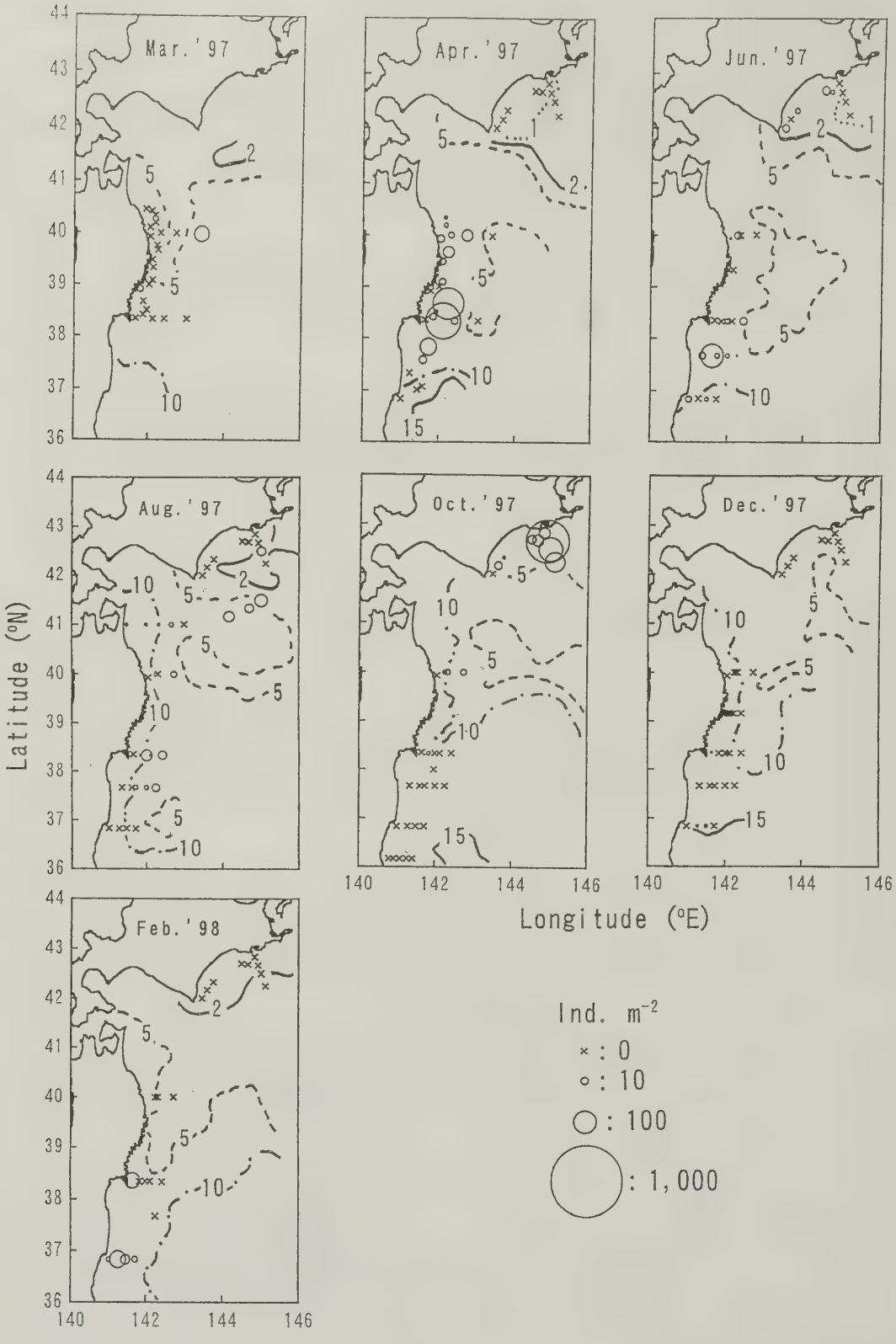

Fig. 3-10. Distribution and abundance of copulated *Euphausia pacifica* females and temperature gradients at 100m depth from March 1997 to February 1998. Numbers indicate temperatures (℃). Scales as in legend.

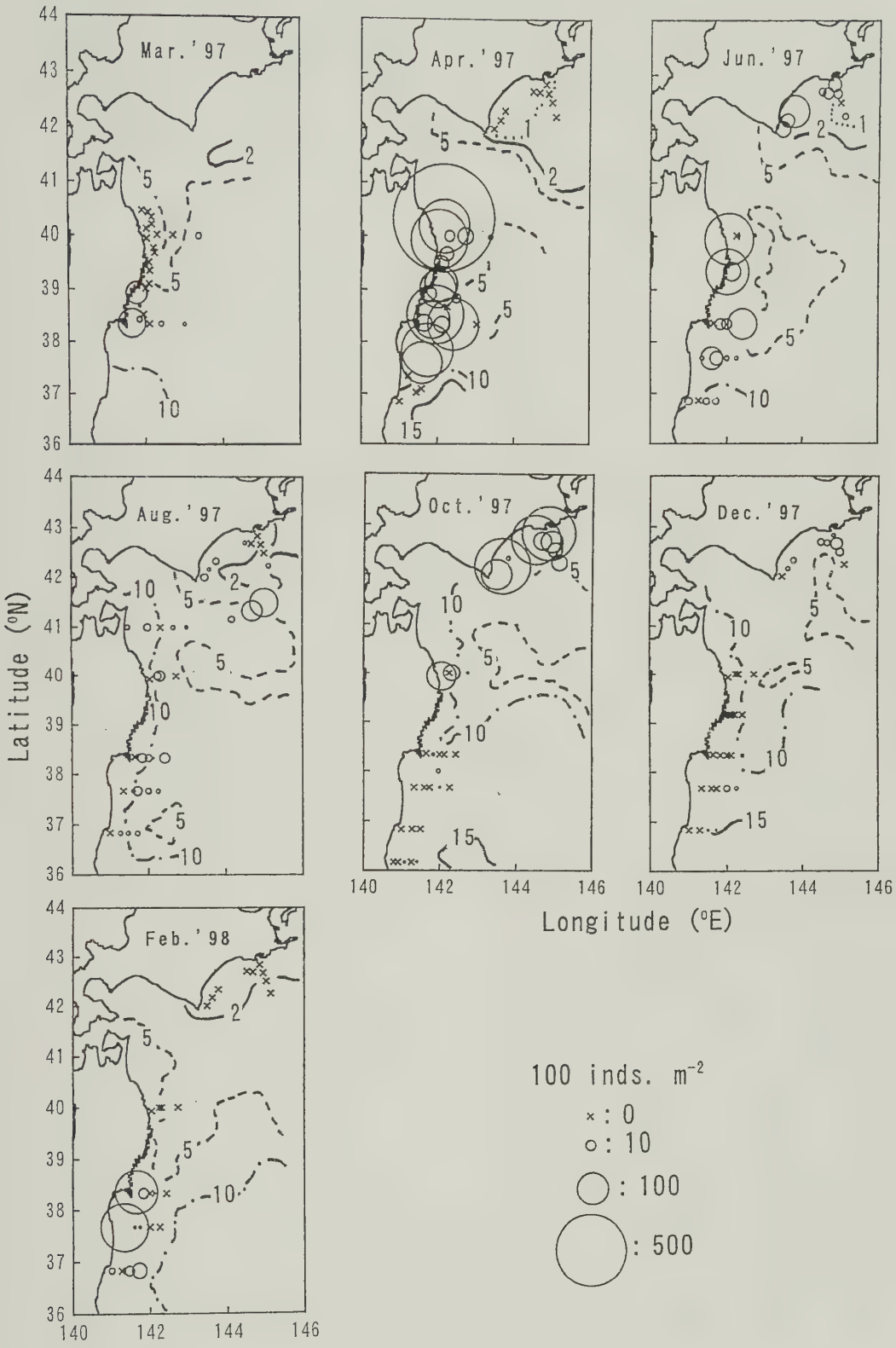

Fig. 3-11. Same as Fig. 3-10 but for eggs.

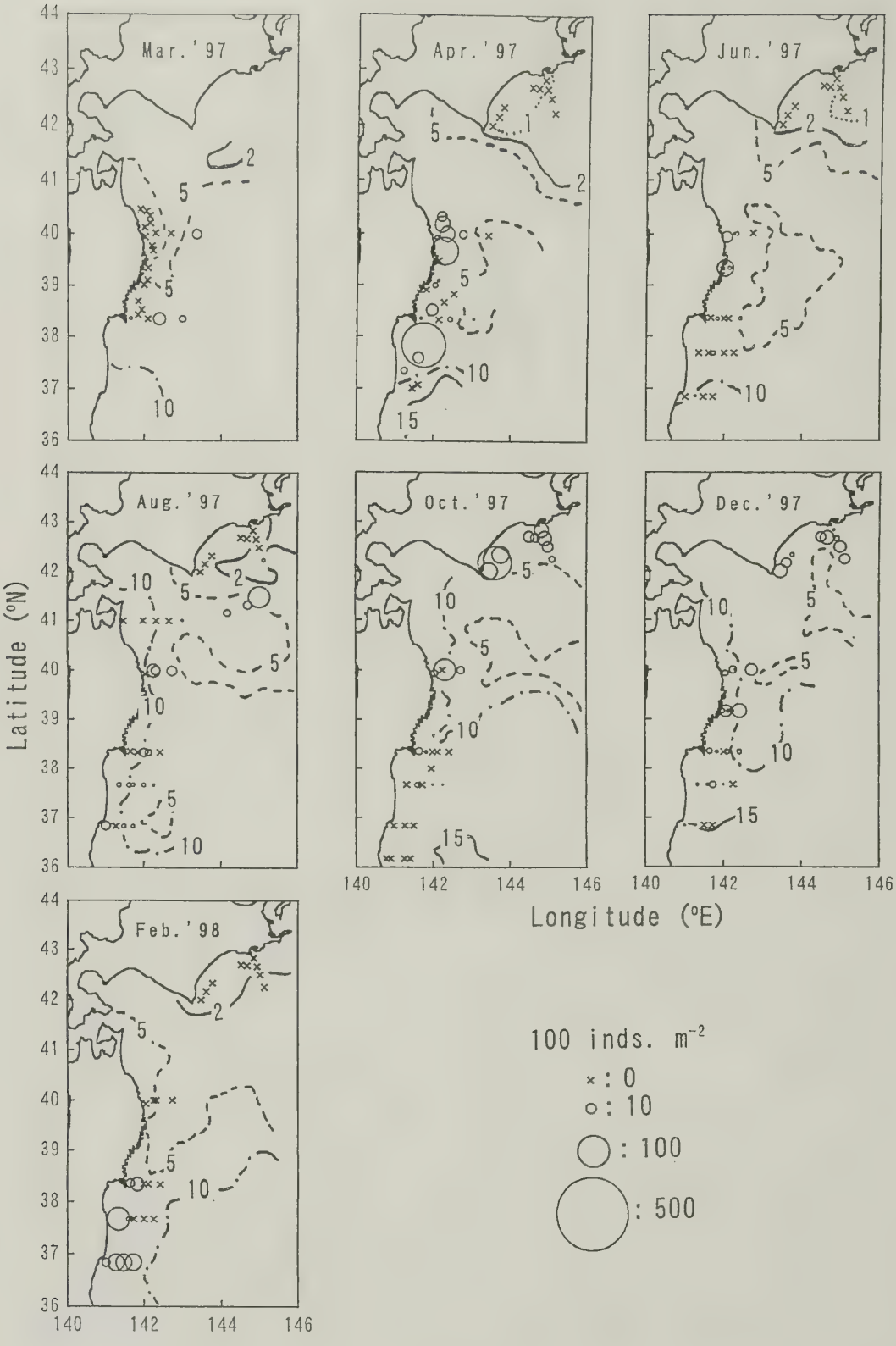

Fig. 3-12. Same as Fig. 3-10 but for calyptopis stage.

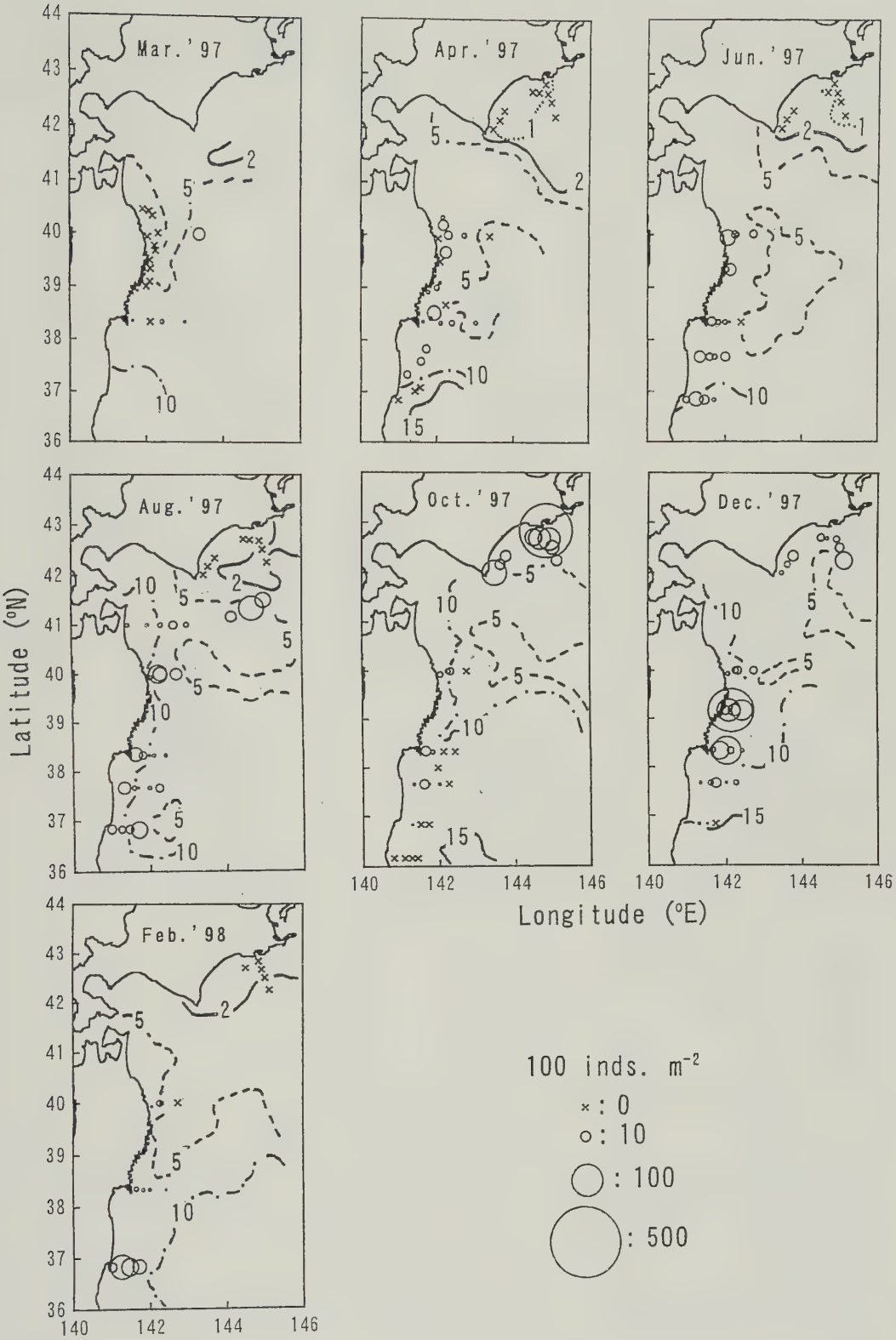

Fig. 3-13. Same as Fig. 3-10 but for furcilia stage.

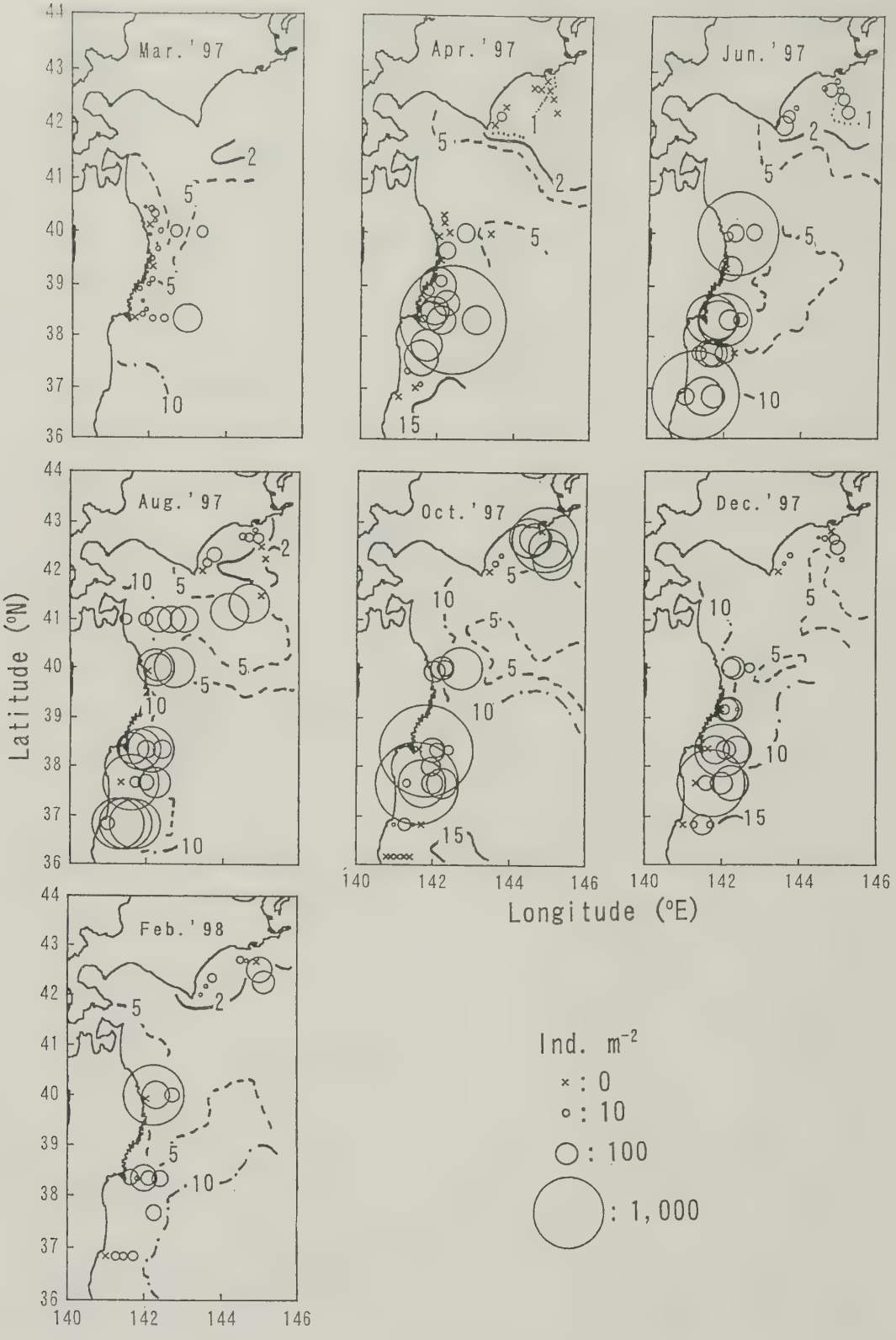

Fig. 3-14. Same as Fig. 3-10 but for immature stage.

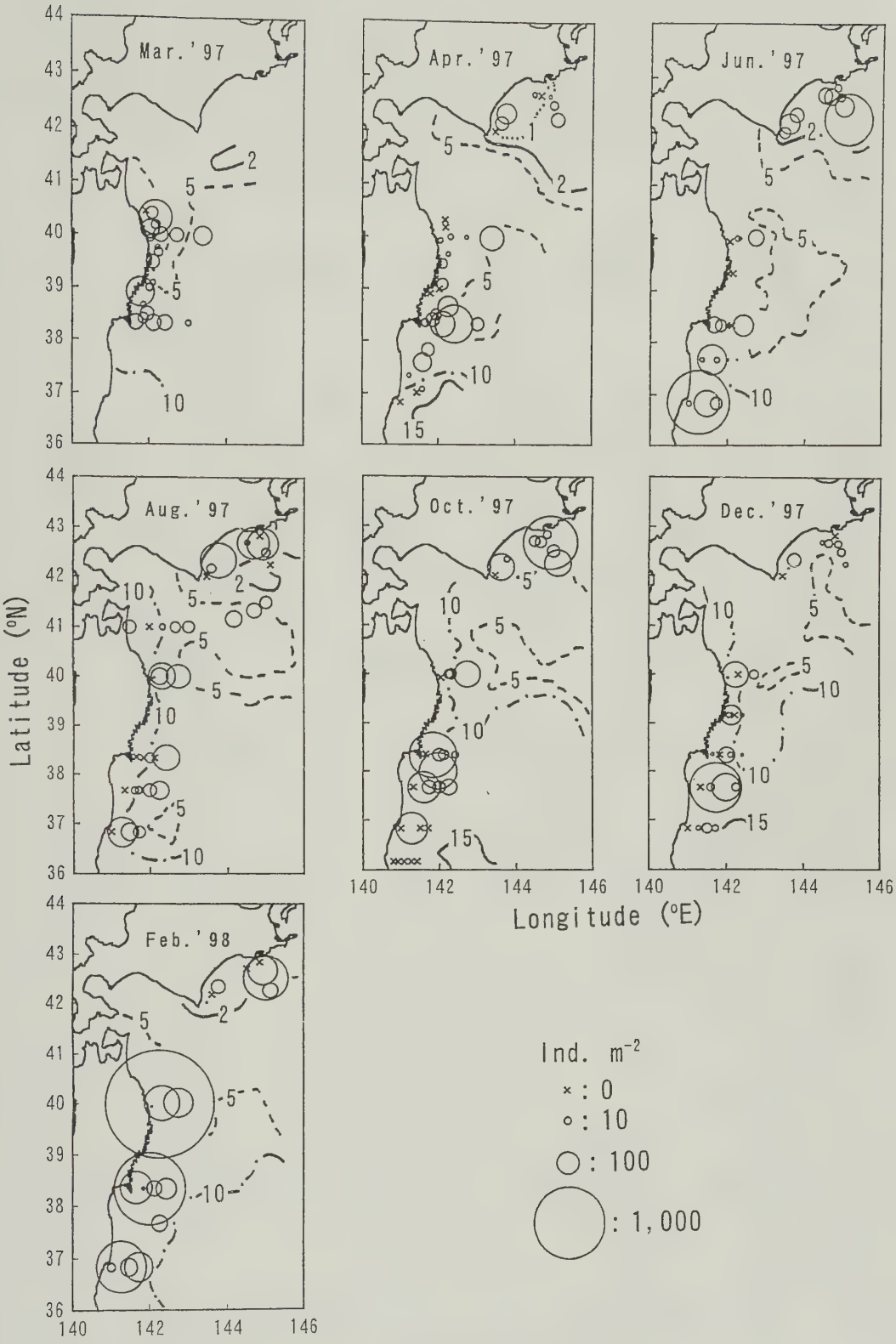

Fig. 3-15. Same as Fig. 3-10 but for small adults.

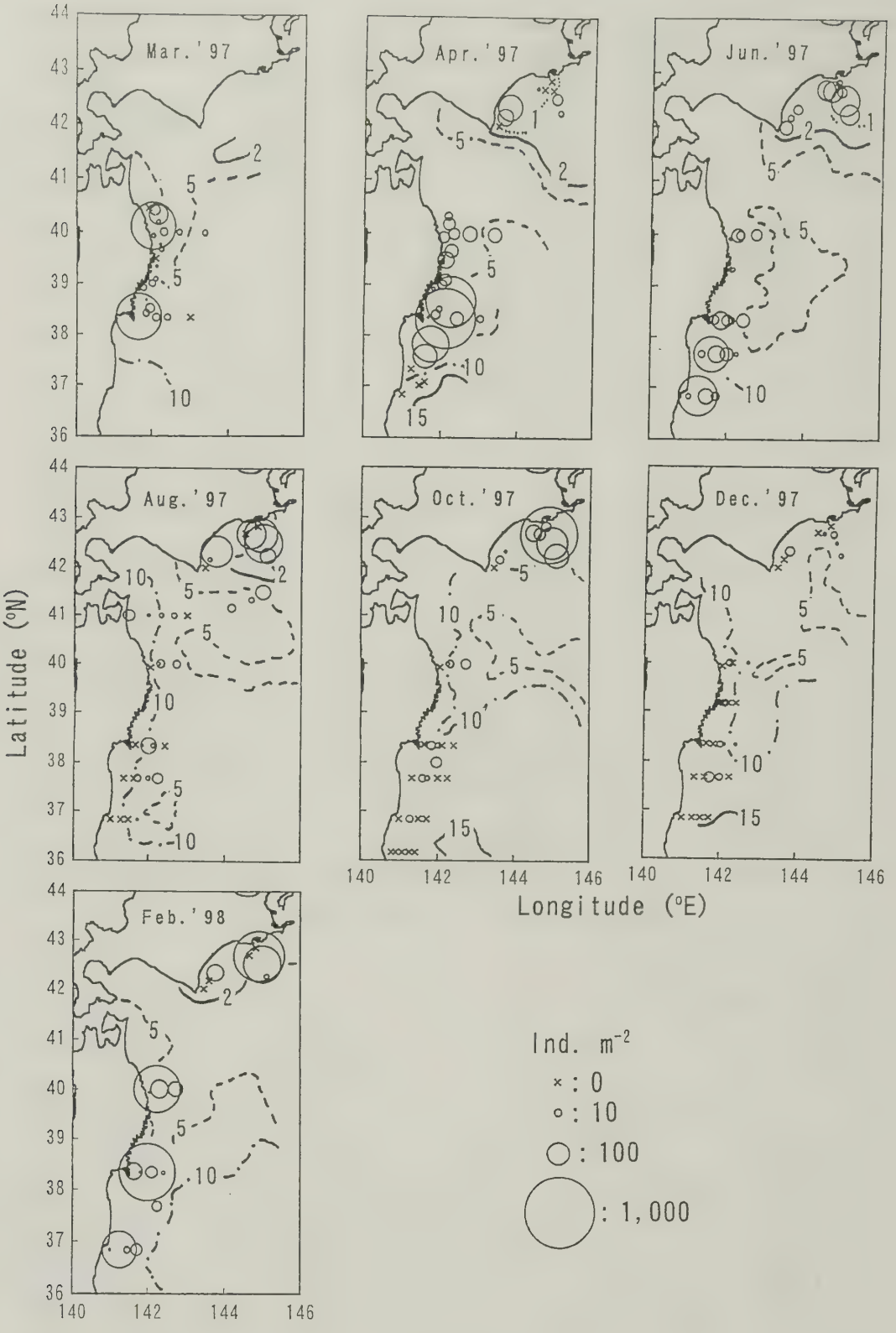

Fig. 3-16. Same as Fig. 3-10 but for large adults.

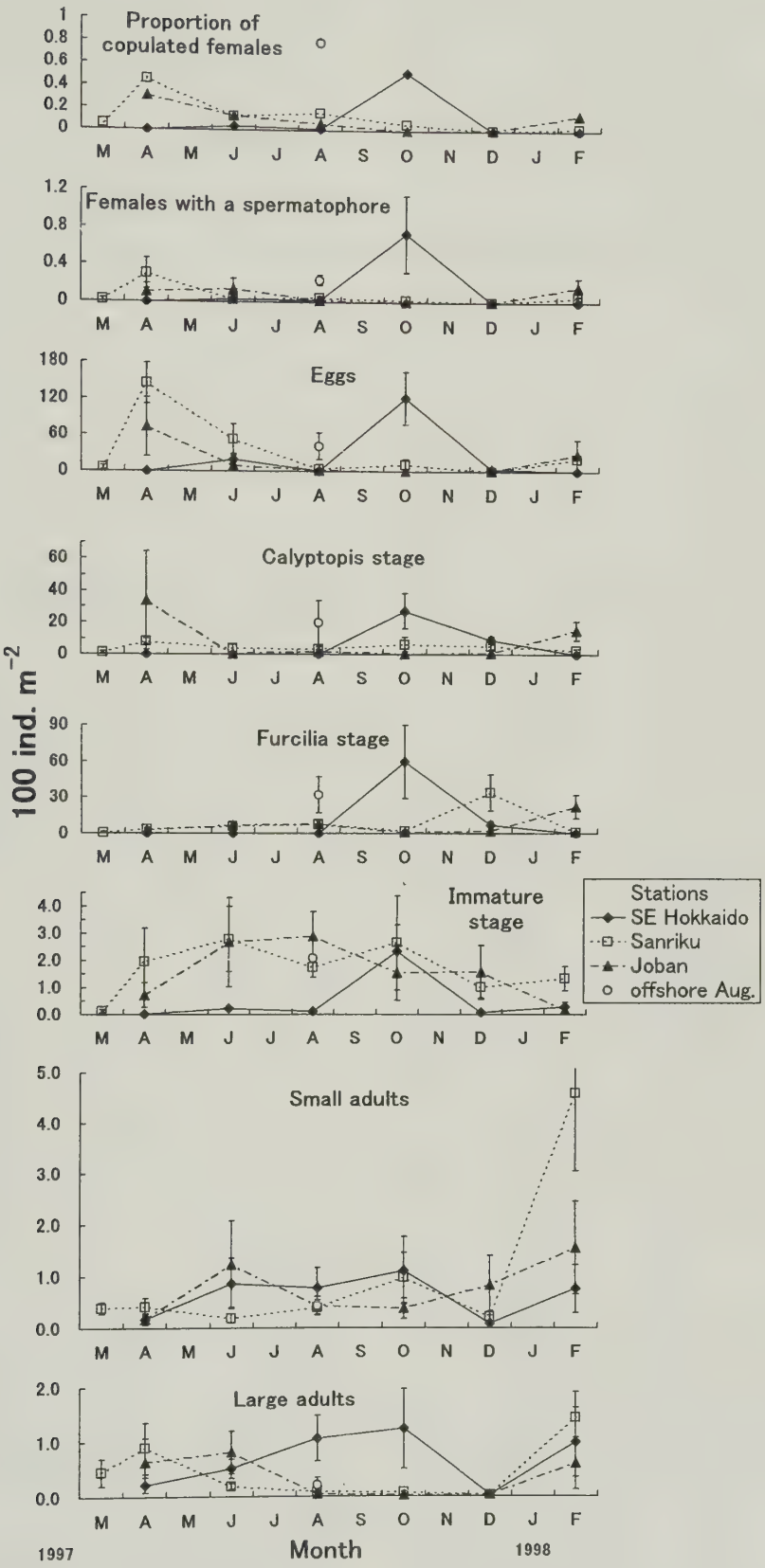

Fig. 3-17. Seasonal changes in the proportion of copulated females and average abundance of each developmental stage of *Euphausia pacifica* by area from March 1997 to February 1998. Vertical bars: ±1 SE.

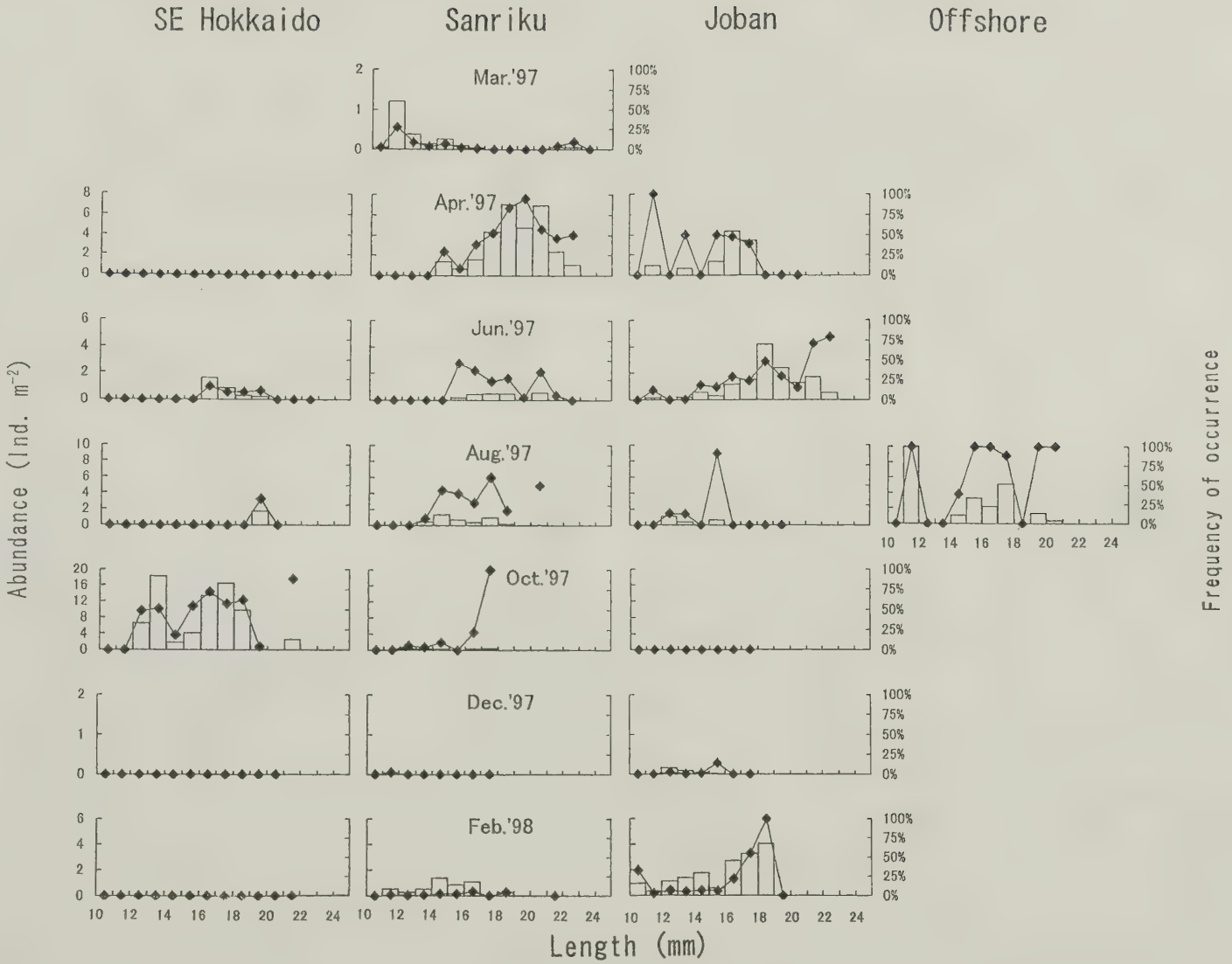

Fig. 3-18. Length-frequency distribution for *Euphausia pacifica* females with a spermatophore (bars) and their frequency (%) to the total abundance of females (solid diamonds) in each region on the basis of cylindrical-conical net samples.

classes off Joban.

Discussion

Seasonal change in spawning and distribution in water masses and life history

Mating and spawning occurred throughout the year in OW and CW, with the main peak occurring in spring and to a lesser extent in late fall-winter on the basis of the Norpac net samples (Fig. 3-4). The main spawning area, which occurred in CW in spring and in OW and CW in summer-fall, agrees closely with to the distributional pattern of large adults. Seasonal changes in abundance of larval and immature stages, which were most abundant in spring-early summer and least abundant in winter, were well synchronized with those of copulated females and eggs. It is therefore suggested that the seasonal activity of spawning depends on the feeding conditions as shown by the high abundances of phytoplankton, microzooplankton and mesozooplankton in spring and low abundances in winter, which are widely recognized patterns in the northern part of the northwest Pacific (Odate, 1994; Kotani *et al.*, 1996; Kasai *et al.*, 2001). This also explains observations in northeastern Pacific waters, where *E. pacifica* reaches its highest spawning intensity during upwelling periods (Smiles and Pearcy, 1971; Brinton, 1976; Heath, 1977; Ross *et al.*, 1982).

Iguchi *et al.* (1993) showed that the modal size (ca. 10mm) of *E. pacifica* hatched in spring indicated no growth from summer to the following winter, but then rapid growth through the following spring in Toyama Bay, southern part of the Japan Sea. Apparent growth in OW and CW, where both larger and smaller adults occurred throughout the year, was recognized from March to June for the smaller group of adults, identical to the growth patterns in Toyama Bay (Fig. 3-8). Such apparent growth was perhaps supported by the favorable food conditions in the region off northeastern Japan as shown by previous reports on seasonal changes in the abundance of phytoplankton, microzooplankton and mesozooplankton (Odate, 1994; Kotani *et al.*, 1996; Kasai *et al.*, 2001).

The negative growth of adult *E. pacifica* during summer and winter was observed both in Toyama Bay (Iguchi *et al.*, 1993) and off northeastern Japan (Fig. 3-8). Iguchi *et al.* (1993) suggested that the negative growth in Toyama Bay was due to the result of the selective death for larger sized individuals. On the other hand, Marinovic and Mangel (1999) documented the shrinkage of *E. pacifica* experimentally. They showed that individuals shrank at temperatures higher than 16.5℃ despite access to excess food. Whether negative growth in *E. pacifica* really occurs in the same conditions (temperatures and food) as experienced during daily vertical migration needs to be examined in the future.

Because spawning and recruitment of larval stages of *E. pacifica* occur throughout the year except for the winter season off northeastern Japan (Fig. 3-4), it is difficult to estimate the age/length relationships from length-frequency distributions precisely. However, the most dense occurrence in abundance of eggs and early developmental stages was observed in April and May, respectively (Fig. 3-4) and two modal cohorts of males and females were consistently recognized in OW and CW (Figs. 3-6 and 7). Endo (1981) estimated that the recruitment time from hatching to adult in *E. pacifica* in Sanriku waters was 2-3 months on the basis of both laboratory experiments and field sampling. Therefore spring hatching and summer recruitment to the adult stage is considered to be the origin of the main cohort off northeastern Japan.

If we connect the April-hatched to the smaller adult cohort in June-July, we can estimate the life span of male and female *E. pacifica* off northeastern Japan to be 24 months and 28 months, respectively. That the life span of females was longer than that of males is identical with that of the Sanriku population estimated by Endo (1981).

On the other hand, a second smaller peak in copulated females and spawning was recognized in summer-fall (Fig. 3-4). It is speculated that hatching in these seasons may greatly contribute to maintaining the population, although this group could not be clearly defined. That is to say, this group hatching compensates for the decrease of the spring hatching by recruiting adults by the next spring, and also spawns during two springs, together with the spring hatching group.

The life span of *E. pacifica* tends to be longer

(2 years old) in colder regions, such as in the sea of Okhotsk (Ponomareva, 1963) and off Kamchatka / south of the Aleutians (Nemoto, 1957) than in warmer regions (at most 1 year), such as off south California (Brinton, 1976). Larger adults, which are thought to over-winter, occurred mainly in OW and CW but rarely in WW throughout the year. So, it appears to be difficult for *E. pacifica* to prolong their life span in warmer water masses off Japan, as has been observed in other warmer regions (Brinton, 1976).

The average abundance of large adults in OW was significantly higher (*t*-test, $P < 0.001$) than those in CW during August and September, but the latter was significantly higher (*t*-test, $P < 0.001$) than the former during March and April (Fig. 3-3). So, they seem to control their distribution according to the seasonal change of the surface temperature. That is to say, they migrate toward OW in summer to avoid high surface temperatures (> ca. 20℃), which would limit their night ascent and reduce both feeding in the euphotic zone and avoidance from mesopelagic predators (see **Chapter 4**); on the contrary, they migrate toward CW in spring to avoid low temperatures throughout the total water column.

Geographical change in spawning and distribution

Geographical distributional pattern of copulation, spawning and recruitment to larval stage in relation to the water masses in the cylindrical-conical net survey generally agrees with those in the Norpac net survey, because they occurred mainly near the marginal area of the Oyashio Current (T_{100} = 5 ℃) throughout the year (Figs. 3-10 and 11). However, copulated females, eggs and larvae were rare or absent throughout the year except in mid fall off southeastern Hokkaido, where extreme cold waters of the Oyashio (T_{100}<2℃) dominated (Figs. 3-10-13). Spawning in such extreme cold waters may be unfavorable for the development of eggs and early larvae as shown in laboratory experiments (Ross, 1981; Iguchi and Ikeda, 1994).

The active spawning of *E. pacifica* is reported to correspond to the phytoplankton bloom period in several locations (Brinton, 1976; Iguchi *et al.*, 1993). In the cylindrical-conical net survey, however, the biomass of phytoplankton shown as the concentration of chlorophyll *a* was lowest off southeastern Hokkaido in fall, where copulated females, eggs and larvae were most abundant like off Sanriku in spring (Figs. 3-9-13). This appears to reflect the second smaller peak in spawning in summer-fall in the wide area of northwestern Pacific by Norpac net survey (Fig. 3-4). Nakagawa *et al.* (2001) suggested that *E. pacifica* can ingest a wide variety of organisms (diatoms, dinoflagellates, tintinnids, invertebrate eggs and copepods) by switching feeding behavior according to the ambient food conditions. Therefore, the variety of food sources used by *E. pacifica* may affect the timing of copulation and spawning season that are closely related to the trophic conditions experienced by this species. On the other hand, active copulation and spawning of *E. pacifica* occurred in OW and CW (Fig. 3-4) or near the marginal area of the Oyashio Current (T_{100} = 5 ℃) throughout the year (Figs. 3-10 and 11). Accordingly, the temperature conditions may be important triggers of copulation and spawning regardless of the season off northeastern Japan.

Results of cylindrical-conical net survey suggest that *E. pacifica* off northeastern Japan gradually adapts to colder areas as the developmental stage progresses from furcilia to adults, and advanced-age adults (large size adult) rarely occur in warmer areas as well as results of Norpac net survey (Figs. 3-13-16). On the other hand, immature stage and small adults existed in all survey areas throughout the year, even off Joban in summer-fall, where the surface water temperatures were relatively high. Immature stage and smaller adults may not ascend toward the surface to avoid the high temperature at night (Iguchi *et al.*, 1993; see **Chapter 4**) and may form benthopelagic aggregations during the day (Nakamura, 1991; Endo, 2000) off Sanriku and Joban in summer-fall. One of the reasons why over-wintered individuals (larger adults) could not exist in such areas is due to the migration toward the colder regions, as suggested in the results of Norpac net survey. Migration ability (= swimming speed) of *E. pacifica* is reported to be up to and potentially in excess of 112m h^{-1} from laboratory observations (Torres and Childress, 1983). This implies that the over-wintered population of *E. pacifica* could migrate horizontally 350km corresponding to the distance

between off Sanriku and off southeastern Hokkaido in 130 days. Besides the horizontal migration to the north, the deeper distribution of adults to avoid the high temperature of the surface layer (Iguchi *et al.*, 1993; see **Chapter 4**) should be considered. For example, around the warm-core ring off Sanriku in July 1995 (SST=23℃ ; St. 10; see **Chapter 4**), the proportion of abundance below 150m depth at night was 10% for small adults and 29% for large adults. However, a deeper distribution of large adults implies the potential for a reduction in the population size, because of forage limitation and predation by mesopelagic and benthic predators as mentioned in the Norpac net survey. These two factors (horizontal migration to the north and deeper distribution) are considered as possible causes of absence of large adults (= over-wintered individuals) in the warmer waters off Sanriku and Joban in summer to fall.

Nakamura (1991) suggested that the fishery-targeted population of *E. pacifica* off Joban in early summer was supplied from the benthopelagic population formed on the continental slope during previous summer and winter. However, most of the fishery-targeted population may be transported by the Oyashio Current, because the abundance of adults abruptly increased both on the continental shelf and slope in February 1998, when the first branch of the Oyashio Current shifted southward to the southern Sanriku area (Figs. 3-15 and 16).

Adults were rare off southeastern Hokkaido in spring (Figs. 3-15-17). The average depth of adult stage was about 150 m in spring during the day, which was shallower than in summer (see **Chapter 4**). The relationship between the abundance of adult stage and average temperature from 0 to 150m showed that the abundance higher than 500 inds. m^{-2} occurred in the waters with temperatures between 2.6 and 8.0℃ , but the abundance was low at <1℃ and >9℃ (Fig. 3-19). The environment off southeastern Hokkaido may be suboptimal for *E. pacifica* where temperatures lower than 1℃ dominated throughout the water column, and therefore they may migrate horizontally toward more southern, warmer areas, which is well consistent with the result in the Norpac net survey. Kodama and Izumi (1994) classified the oceanographic patterns off Sanriku into three types according to the fishing conditions for *E. pacifica*. They suggested that the fishery-targeted population migrate from the Sanriku area to the Joban area, when the Oyashio coastal branch is very strong and comes close to the shore off Sanriku and the suitable temperature area (> 5℃) for *E. pacifica* is restricted to the Joban area. The present study corroborates the conclusions by Kodama and Izumi (1994) except that the lower limit for suitable temperatures (5℃) suggested by them is higher than the lower limit of temperatures (about 3℃) at which high abundances of adults were observed in this study. As mentioned before, it is implied that the *E. pacifica* population could migrate 50 km within 19 days, which nearly corresponds to the distance between the isobaths T_{100} = 1℃ and T_{100} = 5℃ off south Hokkaido in April (Figs 3-15 and 16). Seasonal horizontal migrations of *Euphausia superba* are also reported and the migration is suggested to be induced by spawning (Kanda *et al.*, 1982) and the reduction of intraspecific food competition (Siegel, 1988).

While the *E. pacifica* fishery ground in Sanriku and Joban waters is at its highest abundance in spring, high abundances were also observed off southeastern Hokkaido during summer and fall. It is important to clarify the density and scale of the fishery-targeted populations off Sanriku and Joban in spring compared to off southeastern Hokkaido, using the acoustic method, to examine whether a fishery is feasible or not off southeastern Hokkaido.

Spawning period during the life span

It is suggested that some female *E. pacifica* attain reproductive maturity when they recruit to adult because copulated females occurred among smaller size classes throughout the year off northeastern Japan (Figs. 3-5 and 18), as has been reported in the other warmer areas (Brinton, 1976). If the first spawning age is supposed to be four months after hatching and the non-spawning season is supposed to be during December and March, the spawning period during the life span (28 months) can be estimated to be 18 months, which is considerably longer than that in the other areas (at most 12 months for warmer regions such as off Oregon and southern California).

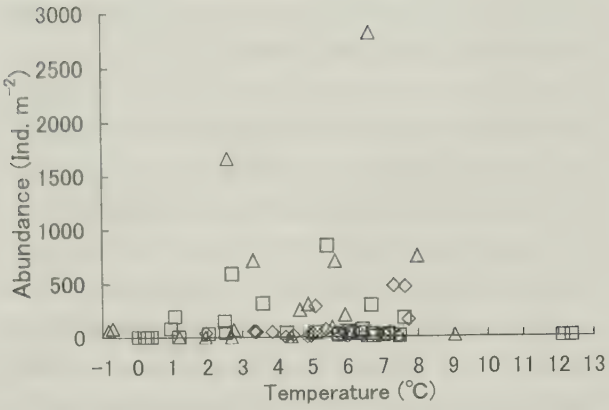

Fig. 3-19. Relationship between the average temperature from 0 to 150m and abundance of adult *Euphausia pacifica* in March (◇) and April (□) 1997 and February 1998 (△).

Chapter 4. Vertical distribution of *Euphausia pacifica*

In northeastern Japan, several studies on the vertical distribution of *Euphausia pacifica* had been carried out (Taniguchi, 1969; Endo, 1981; and Terazaki *et al.*, 1986), but these have been done only at a few fixed stations and the samples are limited seasonally from spring to early summer. Furthermore, the relationship between the vertical distribution and water masses has not been examined until now.

In this chapter, seasonal variations of the vertical distribution of *E. pacifica* were investigated in the coastal and offshore waters off northeastern Japan. At first, seasonal variations of the distribution of pelagic and benthopelagic *E. pacifica* were investigated along the coastal waters off Sanriku using ORI and beam-trawl net samples, and their trophic significance in the coastal water ecosystem off Sanriku is discussed in light of the predator-prey relationships. Secondly, seasonal variations of the vertical distribution of each developmental stage of *E. pacifica* were investigated in the offshore waters off northeastern Japan using MOCNESS-I net samples, and physical and biological factors which determine their vertical distribution of *E. pacifica* were examined.

Materials and Methods

Distribution of pelagic and benthopelagic *E. pacifica* in the Sanriku waters

Six surveys were carried out on the transect line at 50m (St. 1, 10), 100m (St. 2, 9), 150m (St. 3, 8), 200m (St. 4, 7) and 300m (St. 5, 6) isobaths in the vicinity of Kinkazan Island in Miyagi Prefecture (38° 22' N, 141° 32.5' -141° 58'E) from April 1993 to February 1994 on R. V. *Wakataka-maru*, Tohoku National Fisheries Research Institute, Fisheries Research Agency (Fig. 4-1). Sts. 1-5 were surveyed during daytime and Sts. 6-10 were surveyed at night. Water temperatures and salinities were measured by CTD (Neil-Brown) and sea water samples in 6-13 layers were collected at each station using a bucket for the surface sample, and Niskin sampler to measure the concentration of chlorophyll *a*.

ORI net (net mouth diameter: 1.6m; mesh size: 0.33mm; Omori, 1965) was double-obliquely towed from 5m above the sea bed to the surface at 2 knot of the ship speed to collect the pelagic *E. pacifica*. A wireless net recorder (CN-24: FURUNO) was attached on the bridle 2.5m ahead of the mouth of ORI net to monitor the net depth at the bridge. Bongo net (net mouth diameter: 0.7m; mesh size: 0.34mm; McGowan and Brown, 1966) was substituted at Sts. 3-10 in December because of breakage of the ORI net. Beam-trawl net (height: 1m; width: 2m; cod end mesh size: 3mm; no closing mechanism; Nakamura, 1991) was trawled on the sea bed during 10minutes at 1.7 knot of the ship speed to collect the benthopelagic *E. pacifica*.

Samples were preserved with 5% formalin seawater immediately after collection. *E. pacifica* were sorted into immature and adult stages and the lengths (from the tip of the rostrum to the distal end of the telson) were measured to the nearest 0.1mm. The abundance of immature and adult stages for the ORI net samples was calculated using the volume of water passed through the net by a flowmeter (Rigosha) mounted in the mouth of net. On the other hand, the abundance of immature and adult stages for the beam-trawl net samples was calculated using the trawled area on the assumption that all the animals on the area were caught.

Distribution in the offshore waters of northeastern Japan

Samples were collected at stations from 41°30' N to 36°30' N along the 143°E line in late July 1995, mid-April and early September 1998 and late November 1999 on the R. V. *Wakataka-maru*, Tohoku National Fisheries Research Institute, Fisheries Research Agency (Fig. 4-2; Tables 4-1-4). Other samples were collected at about 200m isobath in mid-April and early September 1998. A MOCNESS-I with nets having a mouth opening of 1.4m^2 (about 1m^2 toward the towing orientation) and 0.33mm mesh aperture (Wiebe *et al.*, 1985) was obliquely towed and nets were sequentially opened and closed to sample five stratified layers (0-50, 50-150, 150-250, 250-500, 500-1,000m) in late July 1995 and seven stratified layers (0-25, 25-50, 50-150, 150-250, 250-400, 400-600, 600-1,000m) in mid-April and early September 1998 and late November 1999. Five stratified layers (0-25, 25-50, 50-100, 100-150, 150-170 [or 150-220] m) were sampled for the coastal stations in mid-April and early September 1998. The samples were preserved in 5% buffered formalin seawater immediately after collection. Water temperatures and salinities were measured by CTD (SBE) attached to MOCNESS-I and seawater samples in 6 layers (0, 10, 20, 30, 50, 75m) were collected in each station using a bucket and Niskin sampler to measure the concentration of chlorophyll *a* at each station except late July 1995.

E. pacifica were sorted into its developmental stages except for the nauplius and metanauplius stages, which would pass through nets. The length for the furcilia, immature and adult stages was measured from the tip of the rostrum to the distal end of the telson to the nearest 0.1mm. The abundance of each stage was calculated using the volume of water that passed through the net by a flowmeter attached to MOCNESS-I.

The median depth and 80% range of abundance from the median depth ($D_{80\%}$) for each developmental stage were calculated according to Pennak (1943).

Results

Distribution of pelagic and benthopelagic *E. pacifica* in the Sanriku coastal waters

The coastal branch of the Oyashio Current with low temperatures and salinities came close to the shore and water with 7-8℃ dominated in the total water column at 50-150m isobaths in April (Fig. 4-3). Surface temperature rose after April and attained 18-22℃ in August, but decreased gradually after August. Water with 8℃ dominated in the surface layer at all stations in February. A ther-

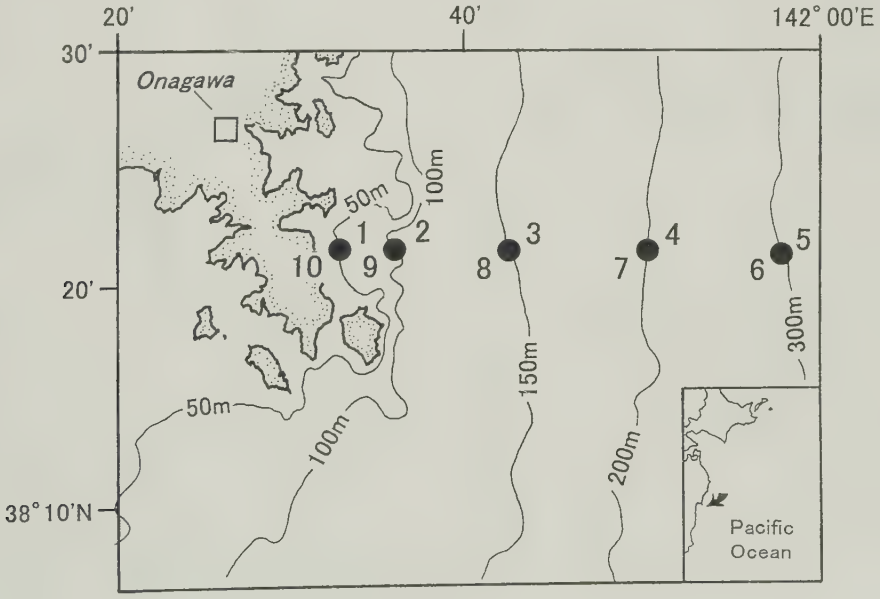

Fig. 4-1. Sampling stations off Onagawa, Miyagi Prefecture from April 1993 to February 1994. Stations. 1-5 were sampled during the day and stations. 6-10 at night.

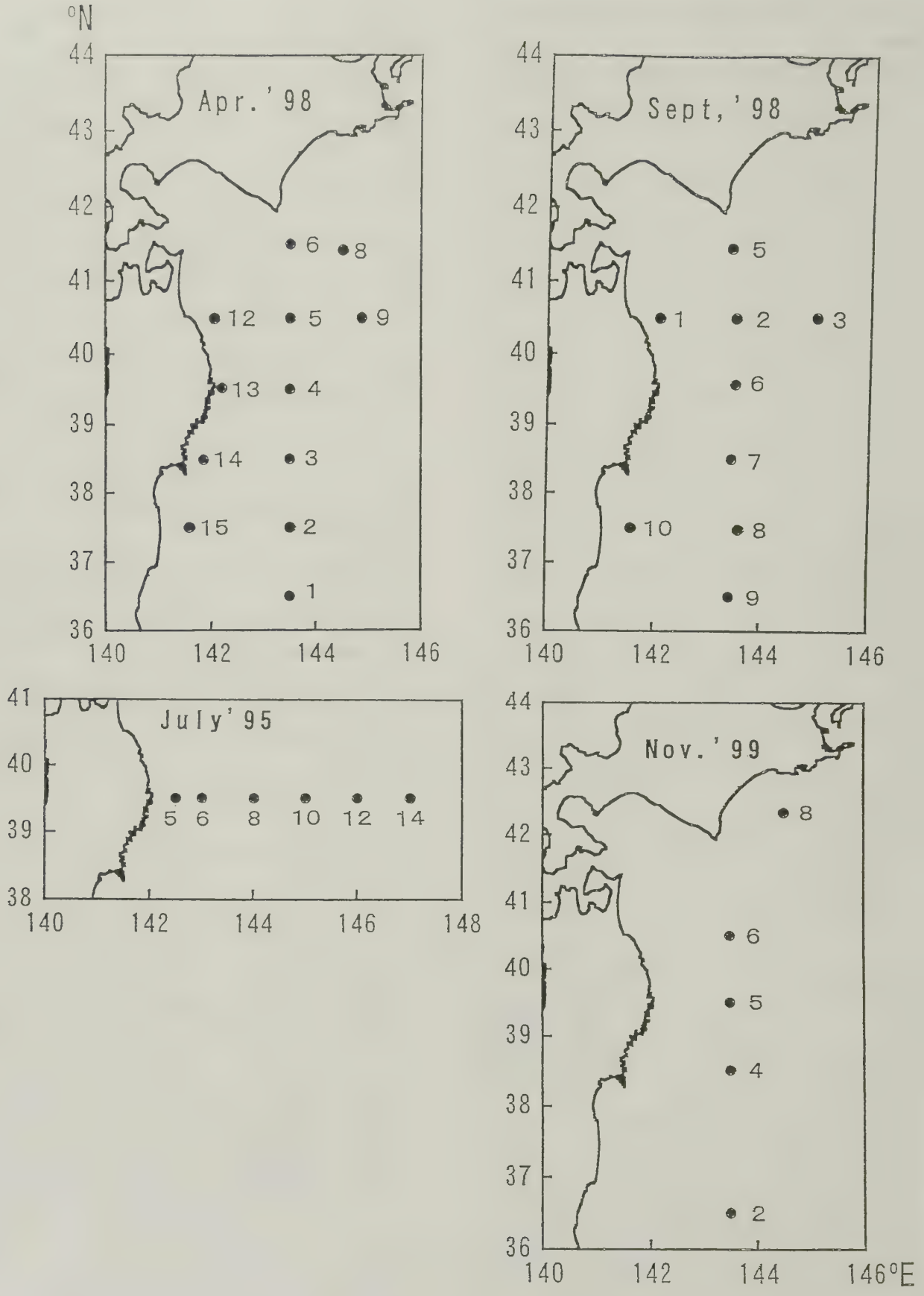

Fig. 4-2. Location of sampling stations using MOCNESS-I in Tohoku waters. Stations are numbered.

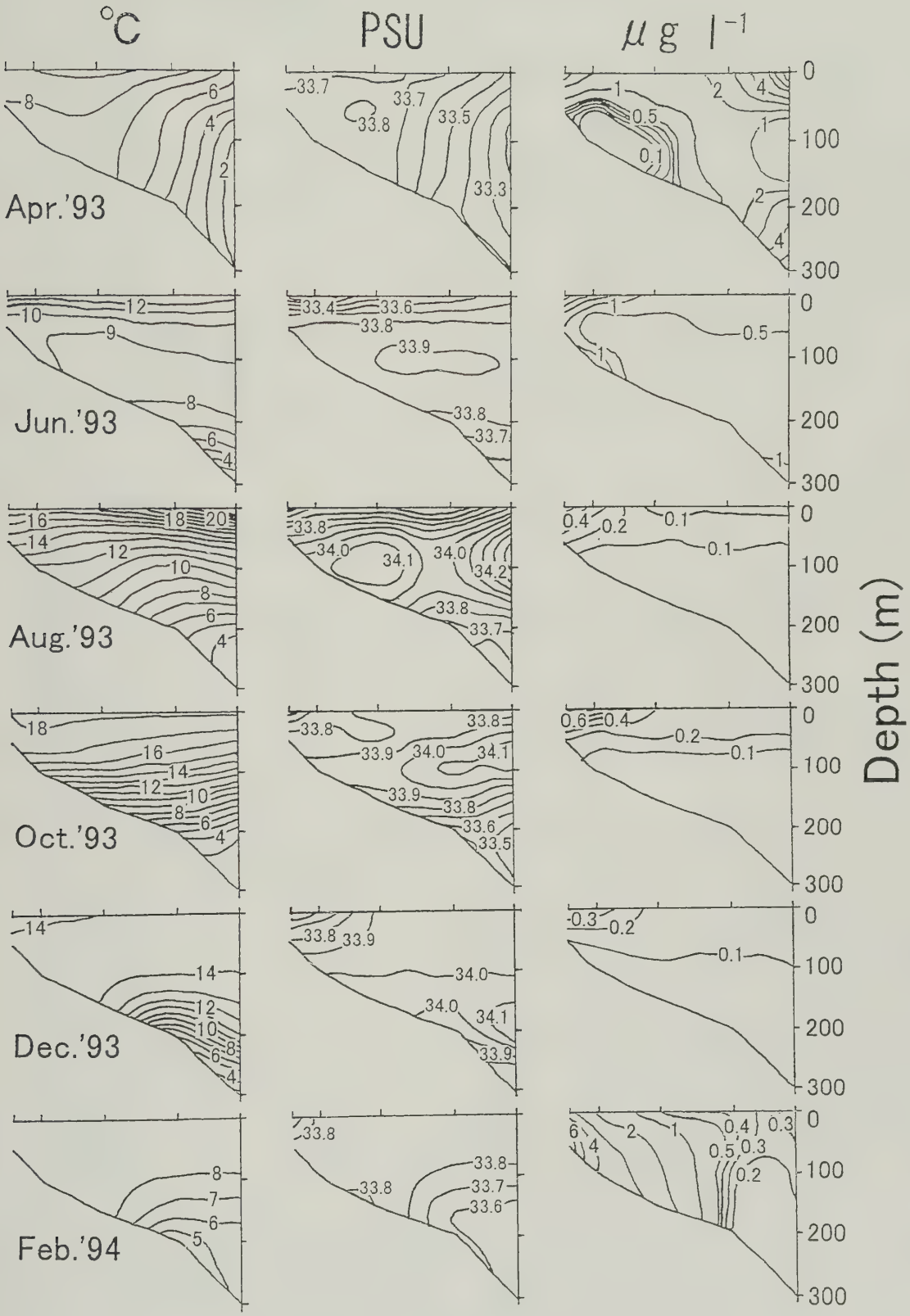

Fig. 4-3. Vertical profiles of temperature (℃), salinity (PSU) and chlorophyll *a* (μ g l^{-1}) off Onagawa from April 1993 to February 1994.

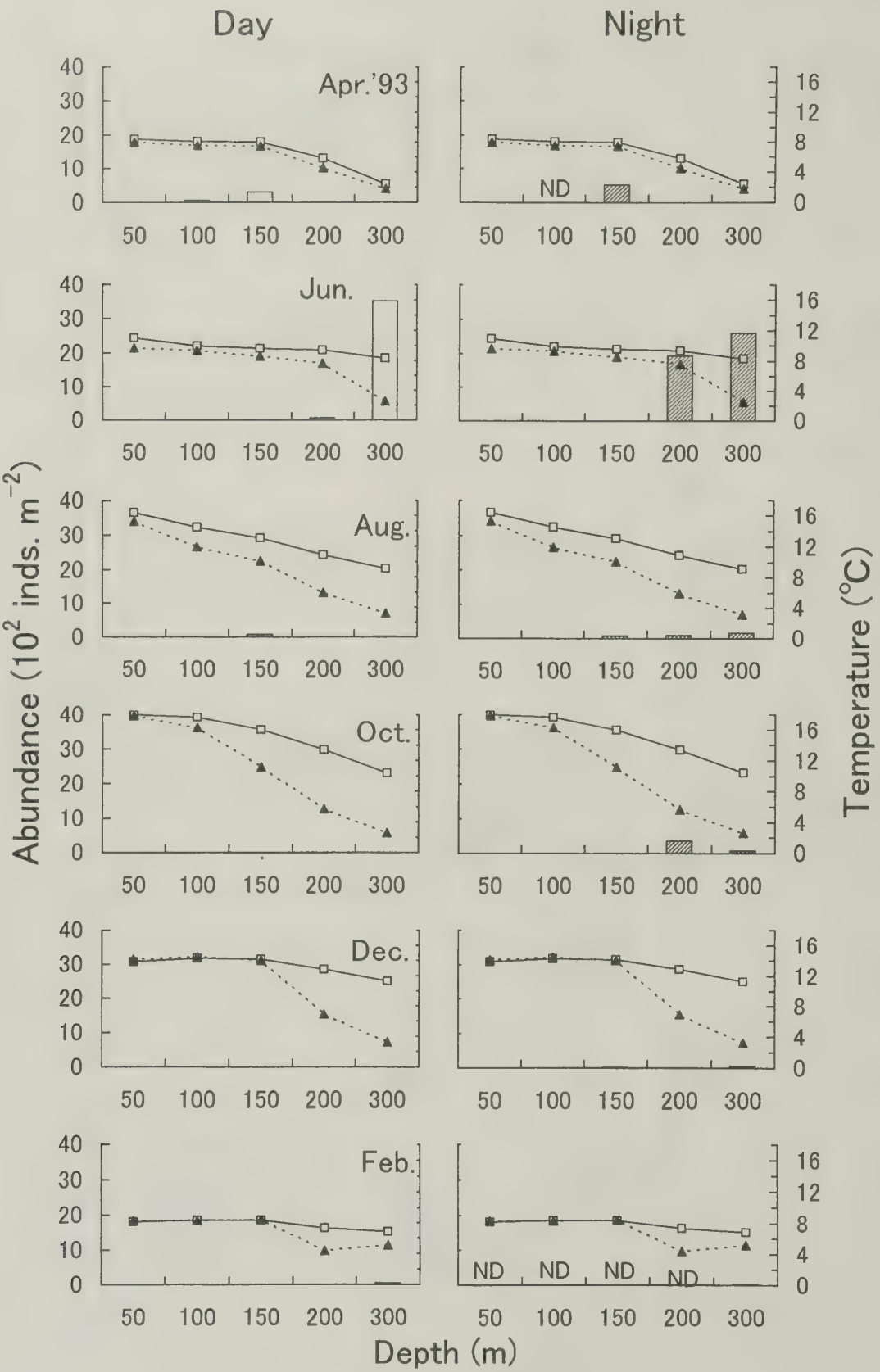

Fig. 4-4. Seasonal changes in the abundance of immature *Euphausia pacifica* sampled by ORI net. Solid and broken lines show the average temperature over the water column from the sea surface to about 5 m above the sea bed and temperature of about 5 m above the sea bed, respectively. ND = no data.

Table 4-1. Locations of stations, times of samplings and sampling depth using MOCNESS-I in Tohoku waters during 17-23 April 1998

St.	Approx. tow location	Date	Depth (m), when towing commenced	Tow time	Tow range (m)
1	36°33'N/143°32'E	17	6,504	7:29-8:58(D*1)	0-23, 23-50, 50-152, 152-252, 252-401, 401-599, 599-961
1	36°35'N/143°30'E	17	6,535	1:13-2:36(N*2)	0-25, 25-50, 50-148, 148-247, 247-401, 401-596, 596-973
2	37°37'N/143°30'E	17	4,201	16:20-17:51(D)	0-17, 17-47, 47-147, 147-246, 246-396, 396-599, 599-987
3	38°33'N/143°25'E	18	2,136	7:31-9:07(D)	0-23, 23-48, 48-148, 148-248, 248-400, 400-599, 599-984
3	38°34'N/143°32'E	18	2,791	1:06-2:16(N)	0-21, 21-49, 49-147, 147-248, 248-401, 401-600, 600-1,000
4	39°35'N/143°27'E	18	2,624	16:05-17:31(D)	0-22, 22-47, 47-146, 146-247, 247-399, 399-600, 600-994
5	40°28'N/143°29'E	19	2,217	7:09-8:26(D)	0-22, 22-47, 47-146, 146-249, 249-400, 400-600, 600-992
5	40°25'N/143°29'E	19	2,226	1:25-3:43(N-DWN*3)	0-22, 22-47, 47-146, 146-248, 248-399, 399-601, 601-980
6	41°26'N/143°30'E	19	1,804	15:31-16:46(D)	0-21, 21-47, 47-149, 149-247, 247-395, 395-596, 596-1,000
6	41°27'N/143°31'E	19	1,717	20:30-22:13(N)	0-21, 21-49, 49-149, 149-248, 248-400, 400-600, 600-993
8	41°25'N/144°37'E	20	4,182	10:58-12:41(D)	0-22, 22-48, 48-151, 151-249, 249-401, 401-597, 597-992
8	41°26'N/144°35'E	20	4,383	21:15-22:52(N)	0-25, 25-48, 48-149, 149-249, 249-400, 400-599, 599-993
9	40°30'N/144°55'E	21	5,997	6:52-8:11(D)	0-25, 25-45, 45-146, 146-247, 247-399, 399-596, 596-991
12	40°30'N/142°03'E	21	214	20:24-20:35(N)	0-24, 24-50, 50-97, 97-147, 147-169
13	39°32'N/142°12'E	22	221	2:07-2:18(N)	0-24, 24-50, 50-95, 95-146, 146-166
14	38°31'N/141°51'E	22	207	9:07-9:20(D)	0-25, 25-50, 50-97, 97-148, 148-165
14	38°31'N/141°51'E	22	204	19:50-20:05(N)	0-25, 25-51, 51-98, 98-149, 149-167
15	37°30'N/141°34'E	23	203	6:20-6:34(D)	0-25, 25-51, 51-99, 99-148, 148-172
15	37°30'N/141°35'E	23	204	1:58-2:10(N)	0-23, 23-48, 48-97, 97-146, 146-172

*1Day, *2Night, *3Dawn

Table 4-2. Locations of stations, times of samplings and sampling depth using MOCNESS-I in Tohoku waters during 22-26 July 1995

St.	Approx. tow location	Date	Depth (m), when towing commenced	Tow time	Tow range (m)
5	39°31'N/142°34'E	22	1,002	7:28-8:14(D*1)	0-47, 47-133, 133-236, 236-499, 499-902
5	39°31'N/142°34'E	23	1,020	0:42-1:24(N*2)	0-47, 47-147, 147-248, 248-499, 499-899
6	39°33'N/143°03'E	22	1,718	17:07-17:53(D)	0-47, 47-146, 146-245, 245-498, 498-995
6	39°29'N/143°02'E	25	1,733	1:59-2:40(N-DWN*3)	0-48, 48-149, 149-248, 248-494, 494-1,000
8	39°30'N/144°08'E	23	5,626	21:44-22:39(N)	0-47, 47-150, 150-250, 250-502, 502-965
10	39°29'N/145°06'E	25	5,508	10:43-11:42(D)	0-52, 52-153, 153-253, 253-502, 502-994
10	39°26'N/145°05'E	28	5,519	0:07-1:18(N)	0-49, 49-145, 145-248, 248-500, 500-999
12	39°30'N/146°07'E	26	5,191	5:34-6:10(D)	0-50, 50-153, 153-248, 248-500, 500-1,000
12	39°29'N/146°05'E	26	5,219	1:05-2:00(N)	0-47, 47-145, 145-246, 246-497, 497-996
14	39°28'N/147°02'E	27	5,211	10:12-10:50(D)	0-49, 49-152, 152-250, 250-502, 502-996
14	39°30'N/146°58'E	26	5,191	22:33-2327t(N)	0-49, 49-152, 152-250, 250-502, 502-996

*1Day, *2Night, *3Dawn

Table 4-3. Locations of stations, times of samplings and sampling depth using MOCNESS-I in Tohoku waters during 1-8 September 1998

St.	Approx. tow location	Date	Depth (m), when towing commenced	Tow time	Tow range (m)
1	40°30'N/142°05'E	1	264	15:56-16:13(D*1)	0-17, 17-23, 23-47, 47-97, 97-150, 150-221
2	40°33'N/143°43'E	4	2,455	8:36-11:56(D)	0-26, 26-51, 51-152, 152-252, 252-401, 401-601, 601-995
2	40°33'N/143°39'E	2	2,354	2:06-4:04(N*2-DWN*3)	0-23, 23-46, 46-151, 151-249, 249-388, 388-575, 575-1,000
3	40°26'N/144°57'E	3	5,977	15:13-17:42(D)	0-26, 26-53, 53-153, 153-254, 254-385, 385-603, 603-1,001
5	41°24'N/143°22'E	3	1,708	12:16-14:24(D)	0-26, 26-53, 53-154, 154-253, 253-402, 402-602, 602-1,042
5	41°24'N/143°21'E	3	1,638	20:50-23:37(N)	0-24, 24-51, 51-148, 148-249, 249-401, 401-602, 602-994
6	39°36'N/143°32'E	4	2,671	20:53-23:25(N)	0-25, 25-49, 49-149, 149-249, 249-400, 400-600, 600-995
7	38°30'N/143°25'E	5	2,745	14:22-16:16(D)	0-24, 24-49, 49-153, 153-254, 254-401, 401-595, 595-1,007
7	38°29'N/143°25'E	5	2,773	20:55-23:12(N)	0-25, 25-50, 50-152, 152-251, 251-400, 400-598, 598-997
8	37°29'N/143°34'E	6	6,073	8:11-10:03(D)	0-25, 25-50, 50-151, 151-252, 252-399, 399-599, 599-1,000
9	36°30'N/143°23'E	7	6,618	7:38-9:21(D)	0-25, 25-51, 51-149, 149-251, 251-398, 398-600, 600-996
9	36°30'N/143°23'E	6	6,669	20:39-22:39(N)	0-26, 26-52, 52-151, 151-250, 250-400, 400-599, 599-988
10	37°28'N/141°34'E	8	205	6:24-6:49(D)	0-25, 25-51, 51-98, 98-149, 149-171
10	37°29'N/141°34'E	7	199	19:15-19:29(DSK*4)	0-24, 24-50, 50-97, 97-147, 147-169

*1Day, *2Night, *3Dawn, *4Dusk

Table 4-4. Locations of stations, times of samplings and sampling depth using MOCNESS-I in Tohoku waters during 26-30 November 1999

St.	Approx. tow location	Date	Depth (m), when towing commenced	Tow time	Tow range (m)
2	36°26'N/143°28'E	26	6,468	8:38-10:51(D*1)	0-24, 24-52, 52-151, 151-251, 251-401, 401-602, 602-1,000
4	38°37'N/143°38'E	27	3,177	22:33-0:01(N*2)	0-25, 25-51, 51-150, 150-256, 256-394, 394-588, 588-757
5	39°20'N/143°25'E	28	2,832	8:48-11:31(D)	0-51, 51-151, 151-251, 251-401, 401-602, 602-995
6	40°23'N/143°40'E	29	2,448	22:02-0:03(N)	0-24, 24-51, 51-152, 152-250, 250-400, 400-600
8	42°23'N/144°50'E	30	1,723	17:27-19:47(N)	0-24, 24-50, 50-150, 150-250, 250-401, 401-599, 599-996

*1Day, *2Night

mocline developed near the surface in August, in 100-200m depth in October and in 200-250m depth in December over the survey area. Chlorophyll *a* concentration was higher than 3 μ g l^{-1} in the surface layer at 50m isobath and in the surface and benthic layers at 300m isobath, but decreased gradually over the survey area from April to December. In February, higher chlorophyll *a* concentration than 1 μ g l^{-1} dominated over the total water column at 50-150m isobaths and a concentration higher than 6 μ g l^{-1} occurred in the benthic layer at 50m isobath.

Pelagic immature stage collected by the ORI net occurred mainly at 150m isobath in April (Fig. 4-4). It was most abundant at 300m isobath in June. It occurred mainly at 200 and 300m isobaths after June, but rarely occurred over the survey area in December and February. Benthopelagic immature stage collected by the beam-trawl net was rarely observed over the survey area in April, but was most abundant during daytime at 300m isobath in June (Fig. 4-5). It occurred mainly at 200 and 300m isobaths after June, but rarely occurred over the survey area in December and February.

Pelagic adults were most abundant at 100m isobath during daytime and 150m isobath at night in April (Fig. 4-6). However it occurred mainly at 200 and 300m isobaths after April. Benthopelagic adults were rarely observed over the survey area in April, but were most abundant during daytime at 300m isobath in June (Fig. 4-7). They occurred mainly at 200 and 300m isobaths after June, but rarely occurred over the survey area in February.

At the coastal stations (100 and 150m isobaths), 15-19mm size classes were dominant to the total abundance both in the pelagic and benthopelagic *E. pacifica* in April (Fig. 4-8). However, <10mm size classes were dominant both in pelagic and benthopelagic *E. pacifica* after June.

At the offshore stations (200 and 300m isobaths), 12-18mm size classes during daytime and 15-21mm size classes at night were dominant in the pelagic *E. pacifica* in April (Fig. 4-9). 15-19mm size classes during daytime and 15-21mm size classes at night were dominant in the benthopelagic *E. pacifica* in April. In June, <10mm size classes occurred abundantly both in pelagic and benthopelagic *E. pacifica* but 15-19mm size classes were most abundant during daytime in the benthopelagic *E. pacifica*. > 15mm size classes gradually decreased in abundance both in the pelagic and benthopelagic *E. pacifica* after August. Then, < 10mm size classes also decreased after December.

Distribution of *E. pacifica* off northeastern Japan in April

Sts. 1 and 2 were located near the warm-core ring centering at 37°10' N, 143°40' -141°58'E (Kato *et al.*, 2000). Surface temperature of these stations was 14.5-17.1℃ (Figs. 4-10-12). The first branch of the Oyashio Current came close to the coastal areas at 38°30' -39°N and 40°N. The thermal front of the Oyashio Current occurred between St. 2 and St. 3. Water with about 1℃ occurred at about 100m depth at Sts. 4, 5, 6, 8 and 9 and lower temperatures than 2 ℃ were dominant from the surface to 100 or 200m at Sts. 6, 8 and 9. Coastal stations (Sts. 12-15) were located near the marginal area of the first branch of the Oyashio Current, and the surface temperatures of these stations were 6.2-8.5℃. The chlorophyll *a* concentration in the surface layer was higher than 1 μ g l^{-1} at all offshore stations except St. 9, especially 0-10m layers at St. 5 and 20-30m layers at St. 6 showed a concentration higher than 6 μ g l^{-1}. The chlorophyll *a* concentration in the surface layer was higher than 1 μ g l^{-1} at Sts. 13 and 15 but lower than 0.7 μ g l^{-1} at Sts. 12 and 14.

Eggs were abundant at Sts. 1, 2, 3 and 5 but scarce at Sts. 6, 8 and 9 and at each coastal station except St. 12 (Figs. 4-11 and 12). Calyptopis was abundant at Sts. 1 and 2 but was scarce at other stations. Furcilia was abundant at Sts. 1 and 12-14, but was scarce at the offshore stations in waters colder than 5℃ isotherm at 100m depth. Immature stage occurred mainly at coastal stations but was scarce at offshore stations. Adults occurred over the survey area including stations in waters colder than 2 ℃ isotherm at 100m depth and were abundant at Sts. 6, 8, 12-15 at night. The abundance of adults collected at night was higher than that collected during daytime for each station except St. 5; especially the abundance collected at night was 452-fold higher than that collected during daytime at St. 14.

In the offshore area, median depth of eggs was shallower than 50m during day and night at each

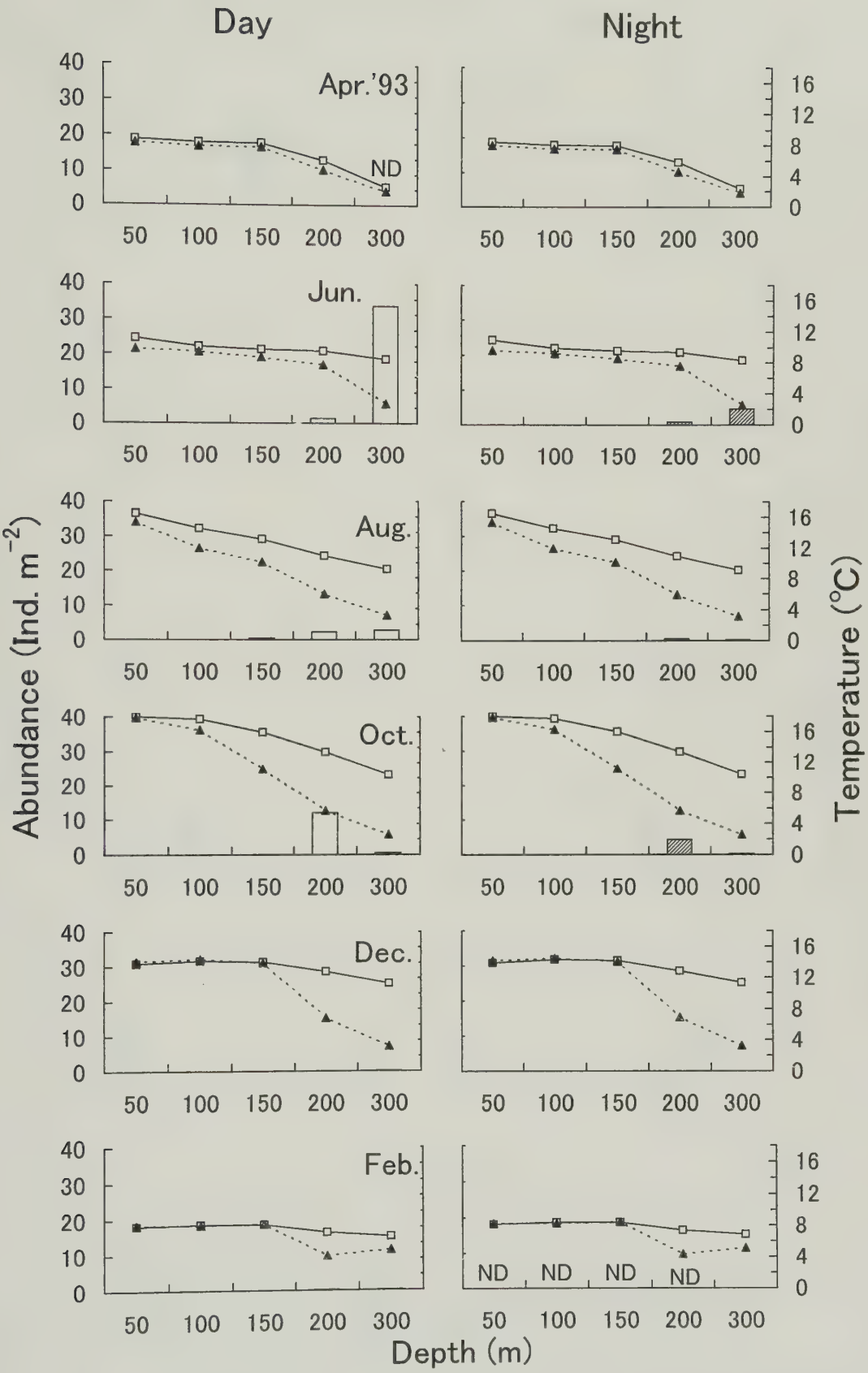

Fig. 4-5. Seasonal changes in the abundance of immature *Euphausia pacifica* sampled by beam-trawl nets. Symbols as in Fig. 4-4.

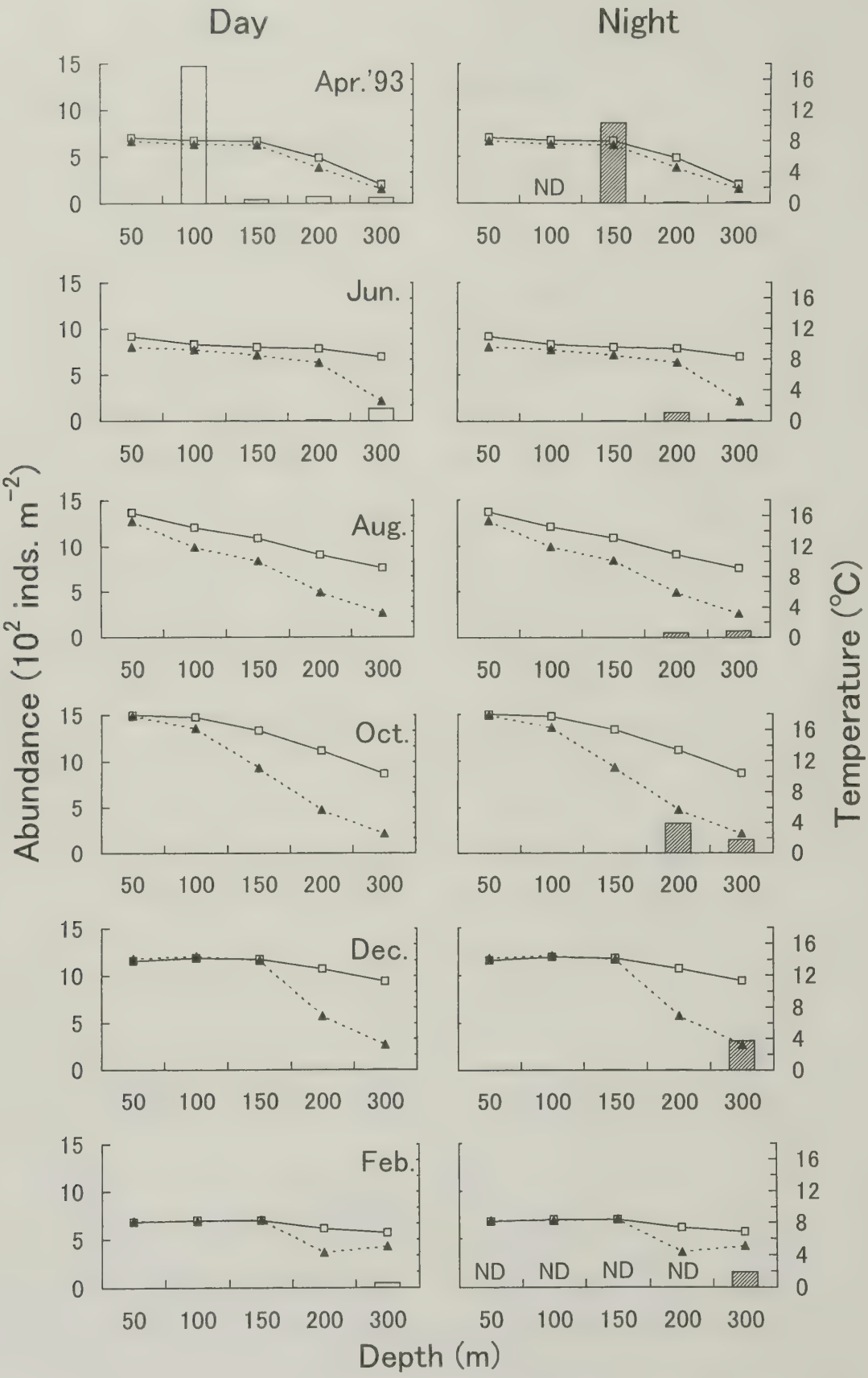

Fig. 4-6. Seasonal changes in the abundance of adult *Euphausia pacifica* sampled by ORI net. Symbols as in Fig. 4-4.

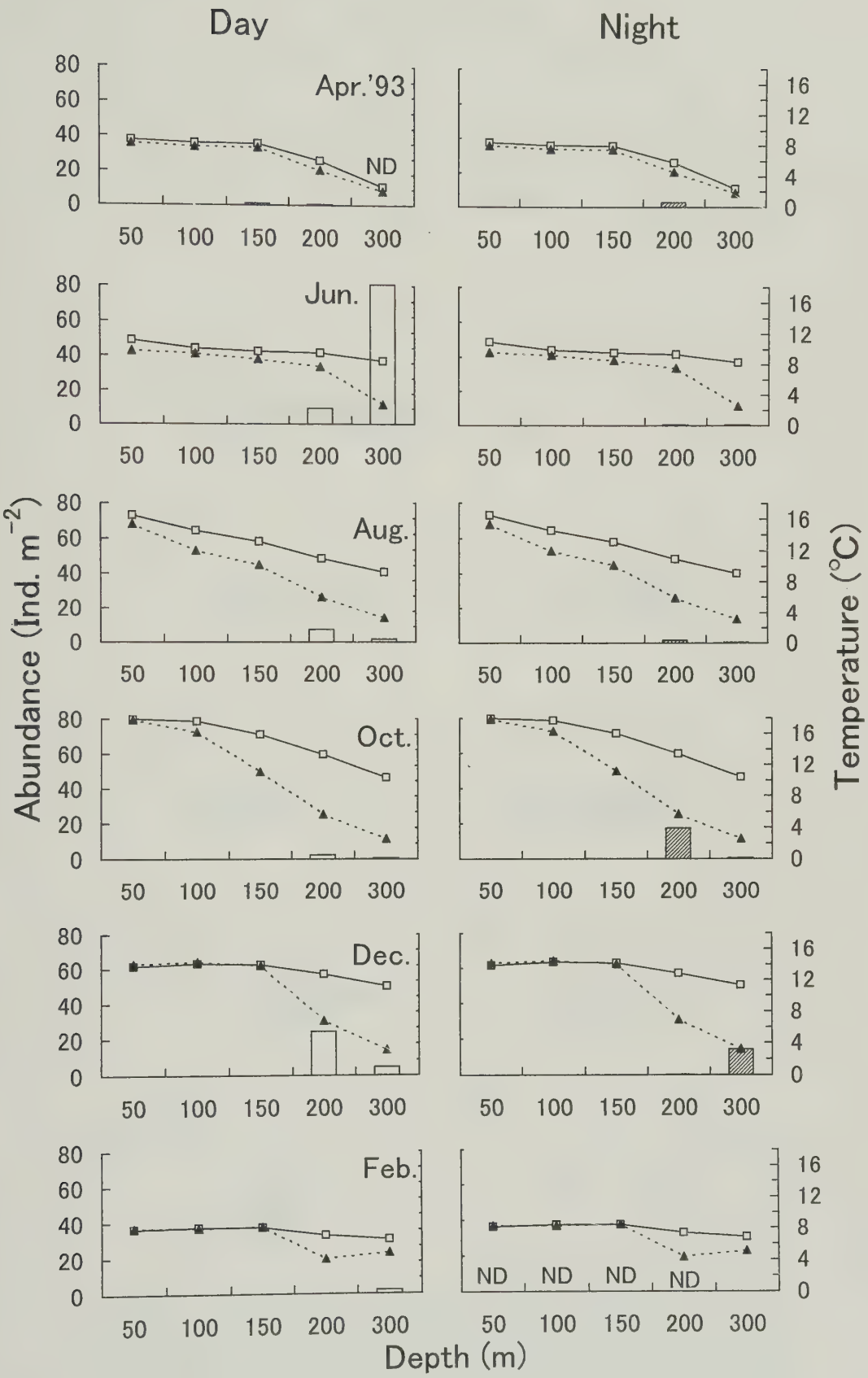

Fig. 4-7. Seasonal changes in the abundance of adult *Euphausia pacifica* sampled by beam-trawl nets. Symbols as in Fig. 4-4.

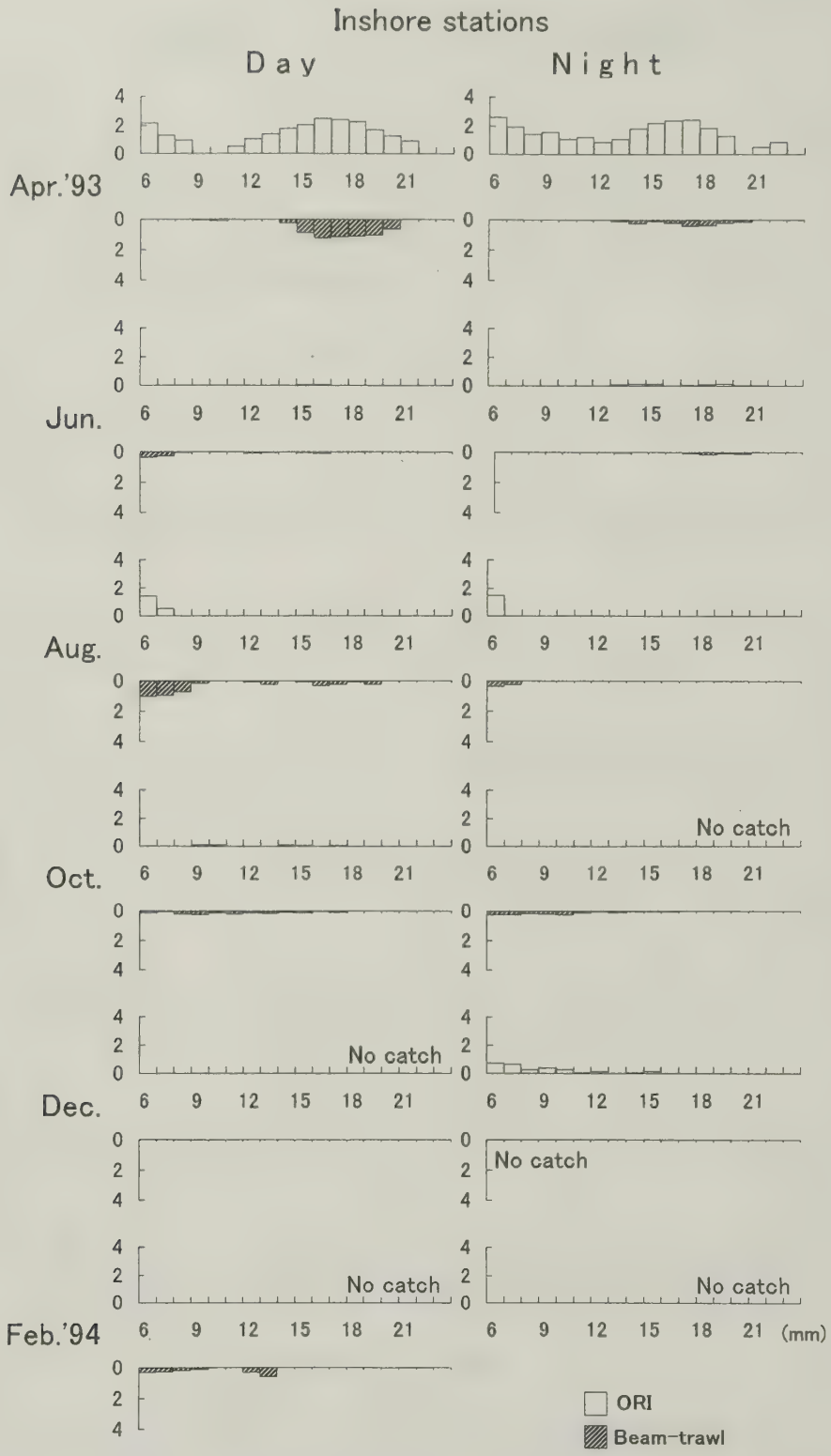

Fig. 4-8. Length frequency distribution of *Euphausia pacifica* at inshore stations (100m and 150m depth). Upward and downward bars show the abundance sampled by ORI and beam-trawl nets, respectively. Vertical bar shows abundance (ORI collection: log (no. m^{-2}+1), Beam-trawl: log (10^2 no. m^{-2}+1)).

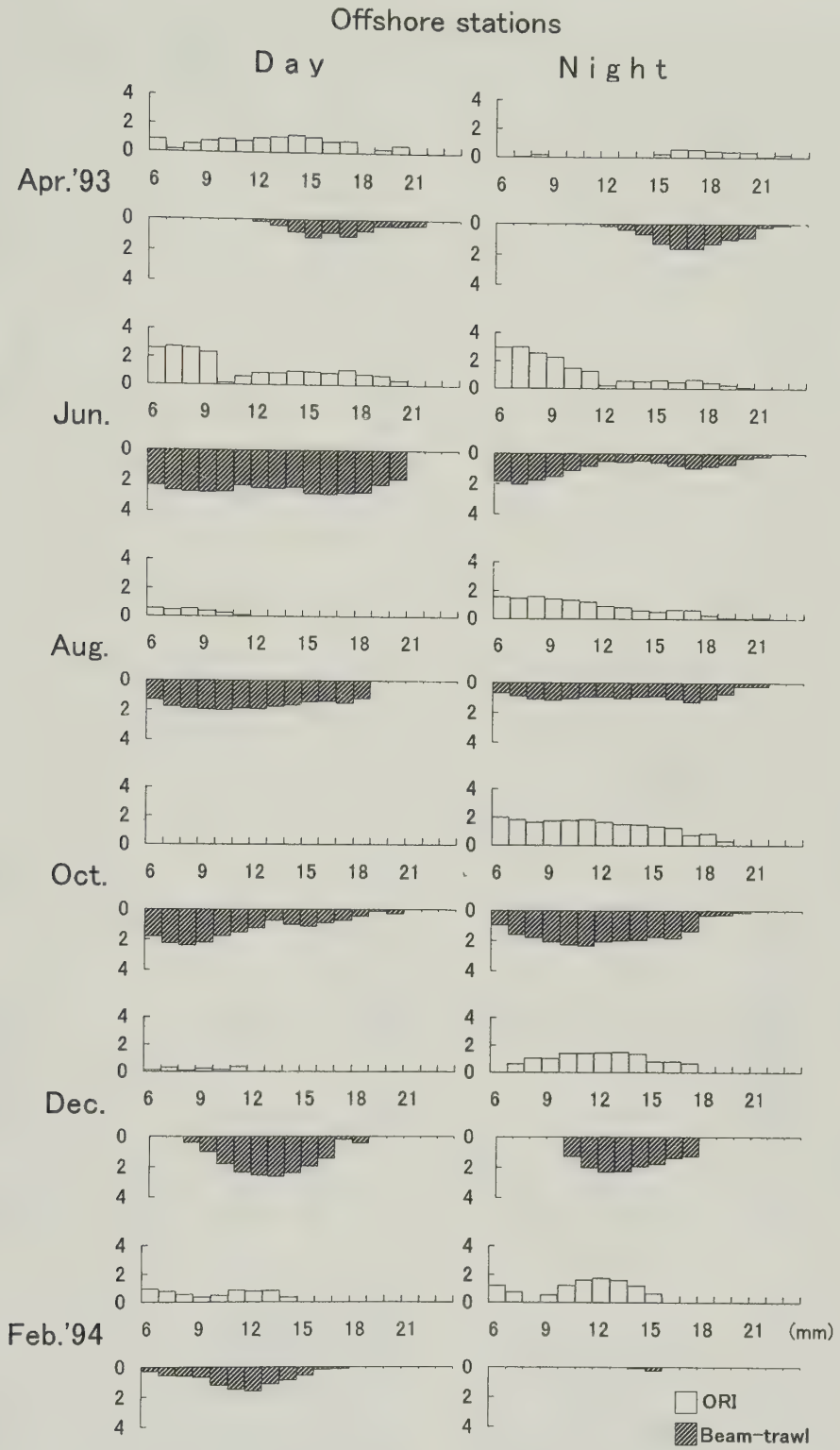

Fig. 4-9. Length frequency distribution of *Euphausia pacifica* at the offshore stations (200m and 300m depth). Upward and downward bars show abundances sampled by ORI and beam-trawl nets, respectively. Vertical bar shows abundance (ORI collection: log (no. m^{-2}+1), Beam-trawl: log (10^{20} no. m^{-2}+1)).

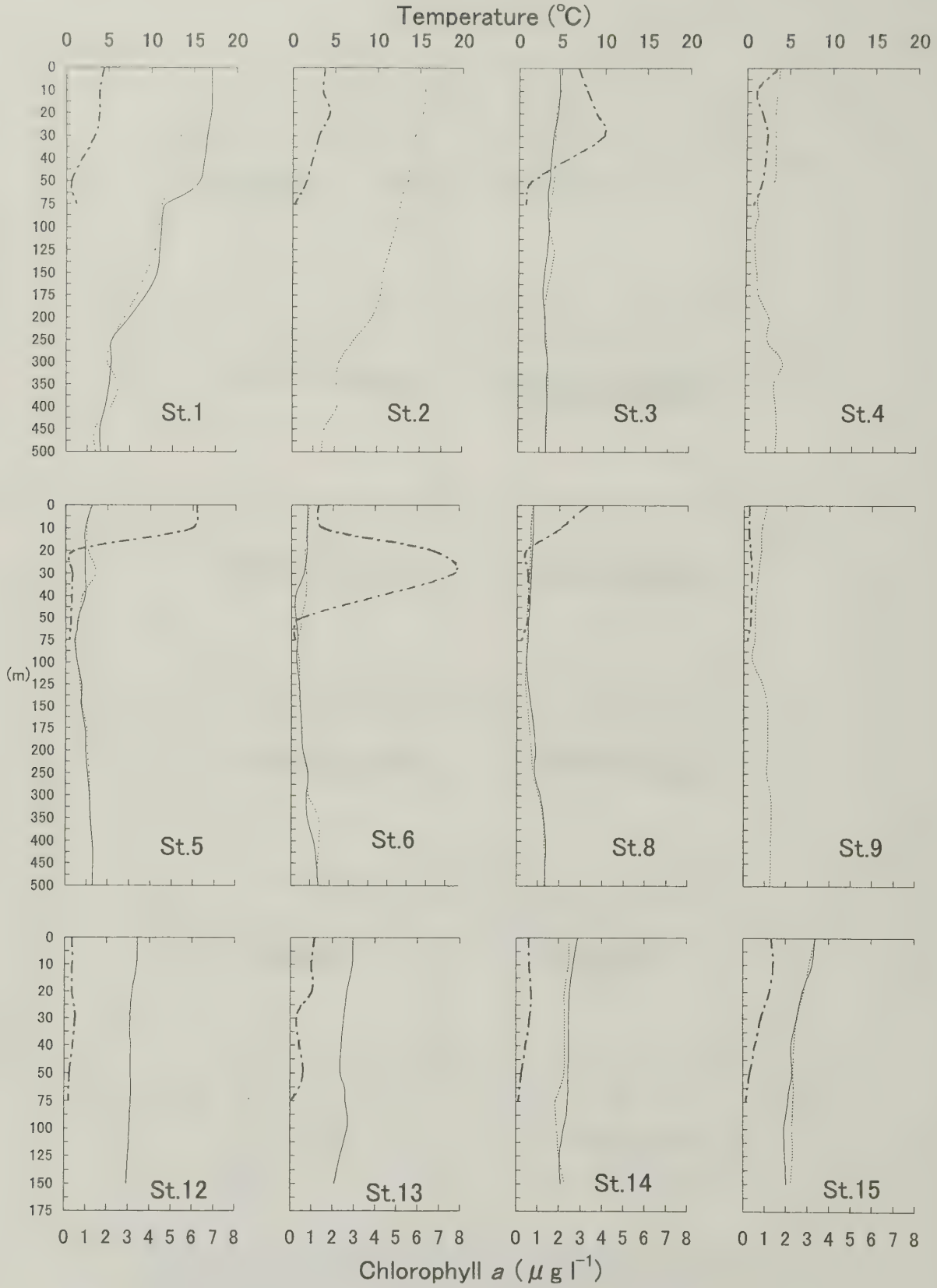

Fig. 4-10. Vertical profiles of temperature and chlorophyll *a* at each station in April 1998. Temperatures obtained from CTD in MOCNESS-I. Chained, solid and broken lines show chlorophyll *a*, night (twilight) temperature and day temperature, respectively.

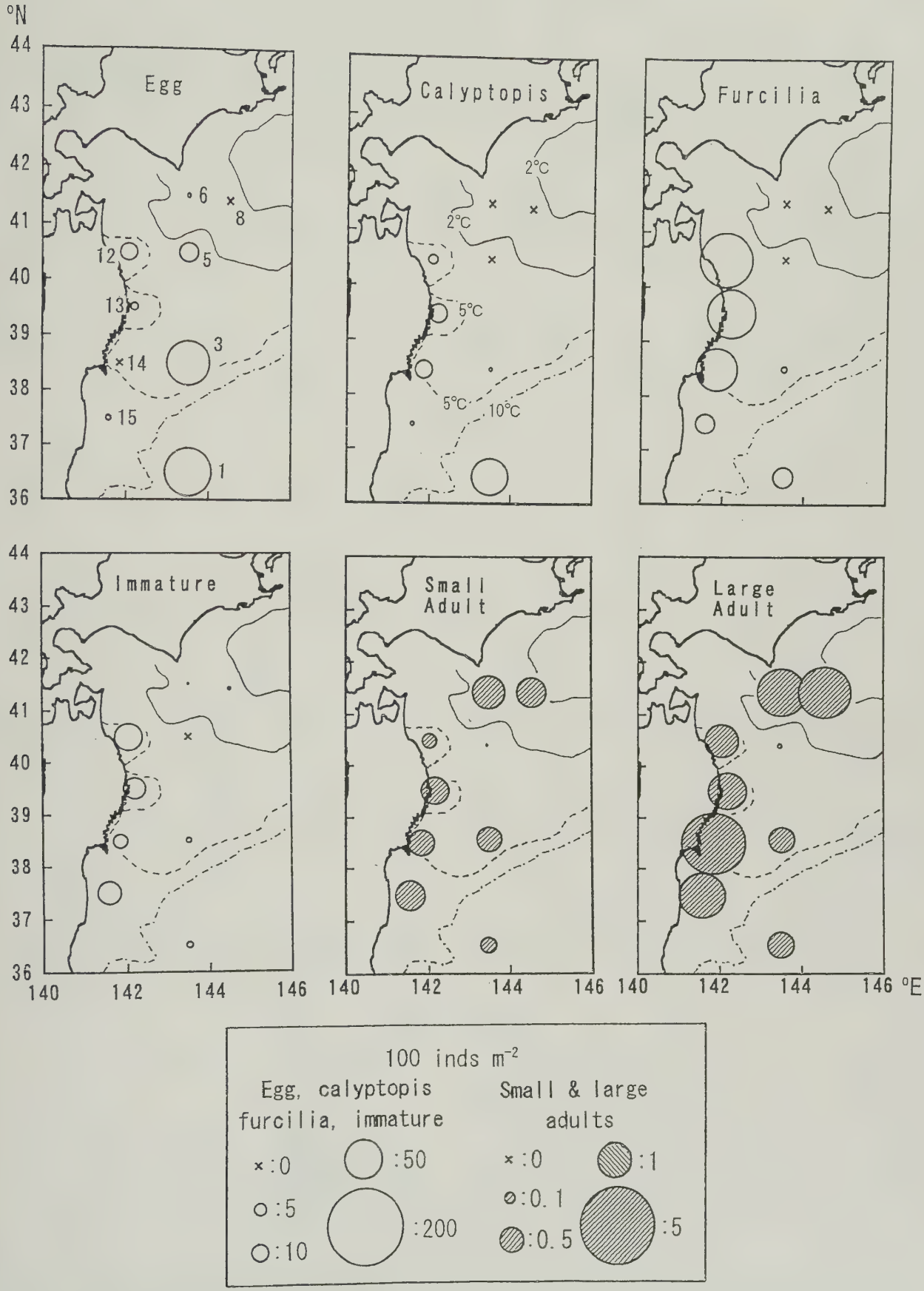

Fig. 4-11. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at night (except for St. 5 at twilight time) and temperature gradients at 100m depth in April, 1998. The scales as in legend. Stations are numbered in "egg".

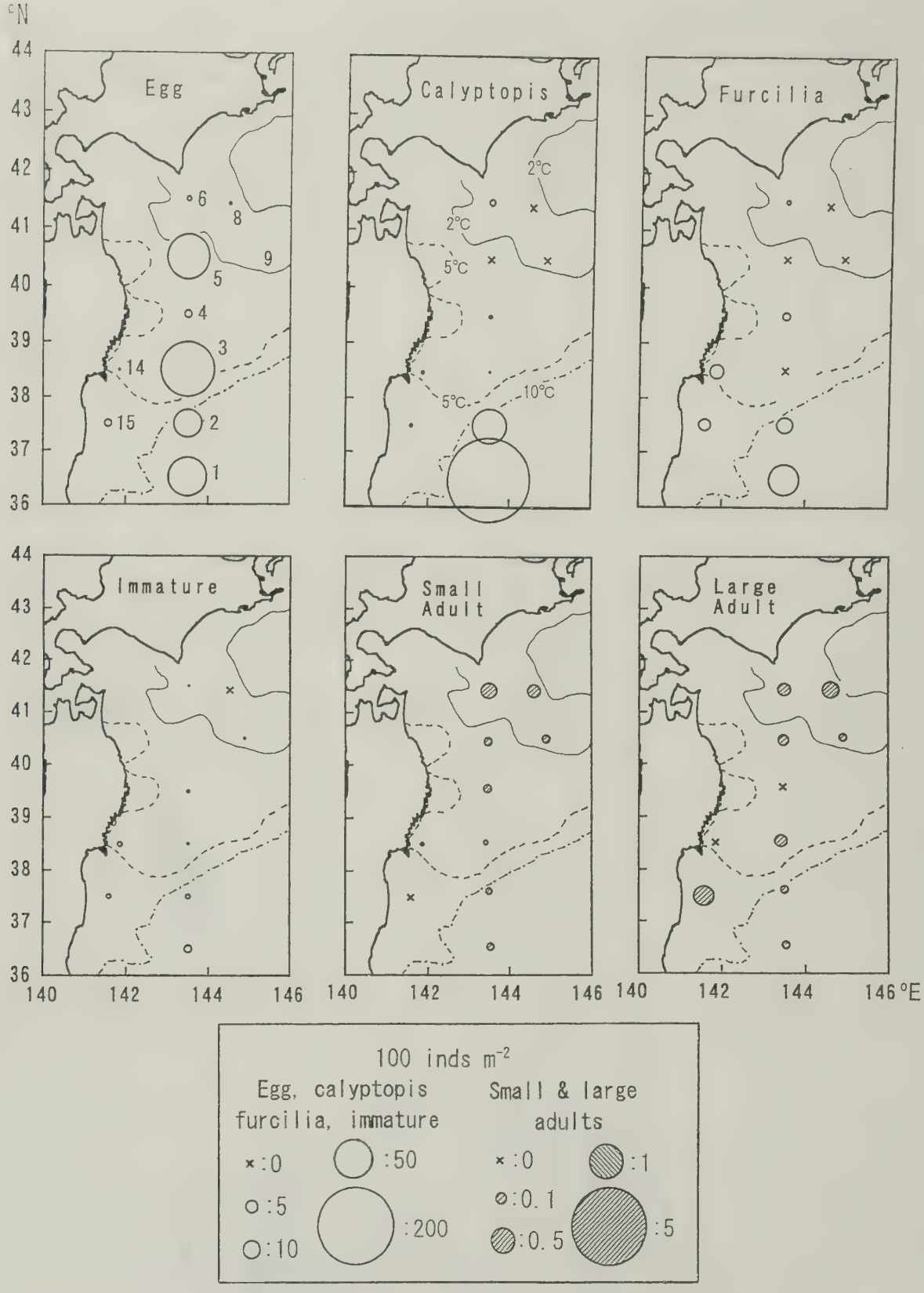

Fig. 4-12. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at day and temperature gradients at 100m depth in April 1998. The scales as in legend. Stations are numbered in "egg".

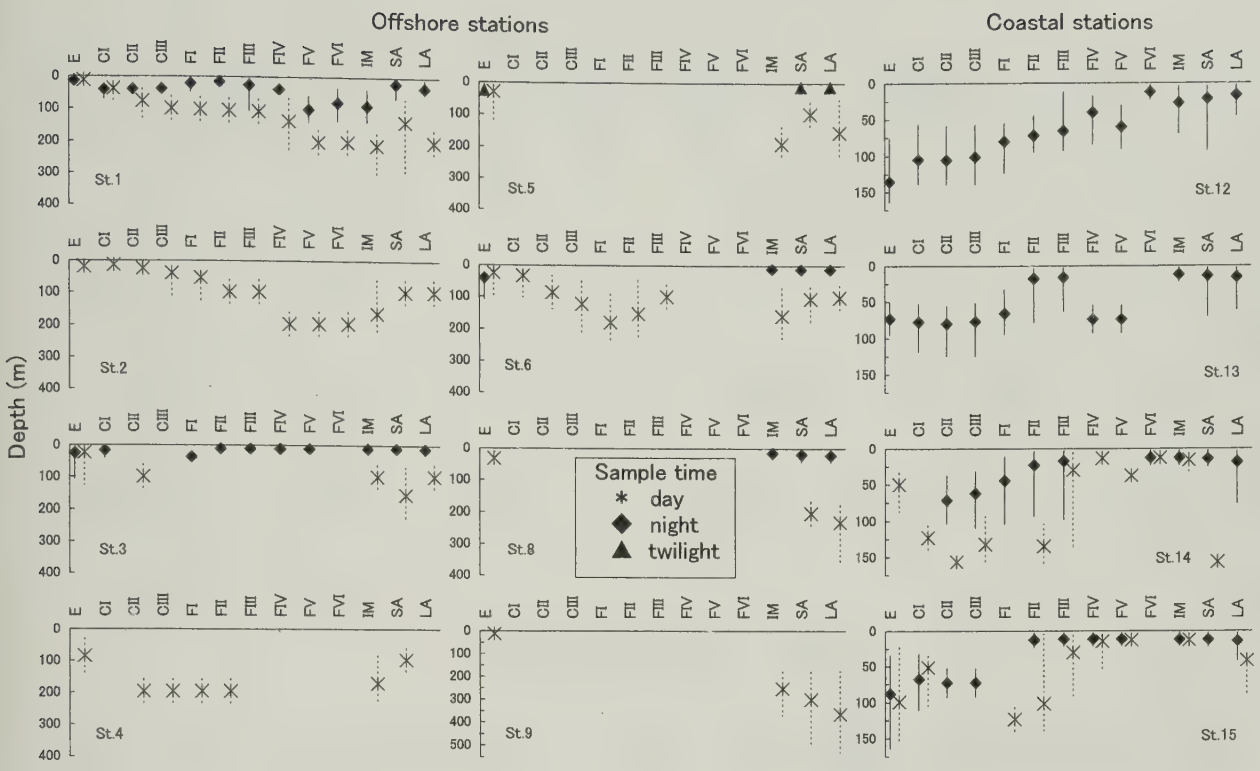

Fig. 4-13. Vertical distributions by developmental stage form egg to adult of *Euphausia pacifica* in each station in April 1998. Symbols show median depth. Vertical bar shows the range of 80% of abundance. SA and LA = small (≦15mm) and large (>15mm) adult, respectively.

station (Fig. 4-13). Median depth of other stages at night was shallower than 50m at all stations except at St. 1 where median depth of fifth and sixth furcilia and immature stage occurred at about 100m depth. Median depth of first calyptopis during daytime was also shallower than 50m at all stations, but median depth during daytime tended to increase with the developmental stages from second calyptopis. However, the deepening trend with developmental stages stopped at about 200m depth from fifth furcilia at St. 1, sixth furcilia at St. 2, second calyptopis at St. 4 and first furcilia at St. 6. Median depth of adults during daytime was generally at 100-200m but at about 300m at St. 9.

In the coastal area, median depth of eggs was deeper than 50m during day and night at each station (Fig. 4-13). Median depth of calyptopis at night was deeper than 50 m and deepest among all developmental stages except eggs at each station. Median depth of later stages than furcilia at night tended to be shallower with the developmental stages and median depth of immature and adult stages was shallower than 25m at each station. Depth of the lower limit of 80% abundance in calyptopis and first to third furcilia during daytime was deeper than 100m at Sts. 14 and 15 and their median depth was deepest among all developmental stages. Median depth of later stages than third furcilia during daytime was shallower than 50m at each station except at St. 14 where median depth of small adults were at about 150–170m. Median depth of large adults during daytime was at about 40m at St. 15.

Distribution of *E. pacifica* off northeastern Japan in July

It appears that Sts. 6, 8 and 10 were located at the northern side of the warm-core ring (Inagake *et al.*, 1997), with St. 8 closest to the center of the ring among these stations (Figs. 4-14-16). St. 5 was located within the influence of the first branch of the Oyashio Current while Sts. 12 and 14 were under the influence of the second branch of the Oyashio Current. A strong thermocline appeared between 0 to 50m and water cooler than 2.9 ℃ occurred below 50m. Eggs were abundant at St. 10 during daytime and St. 5 and 14 at night (Figs. 4-15 and 16).

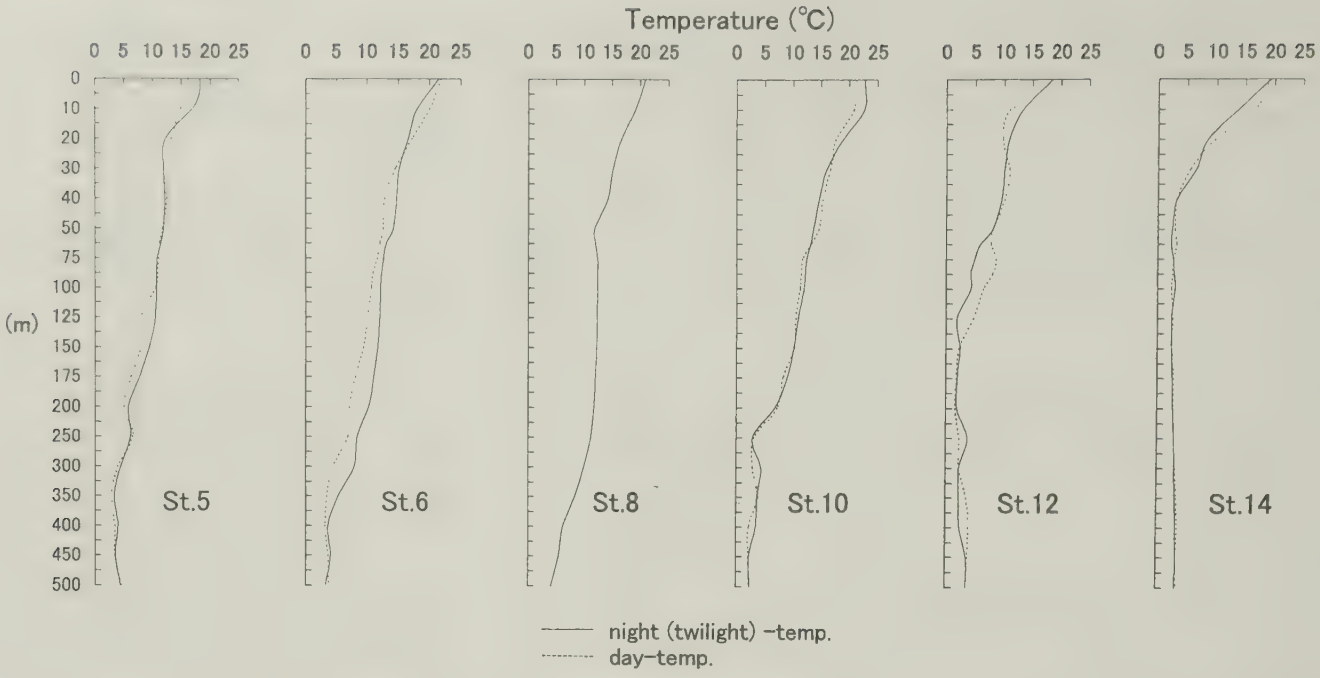

Fig. 4-14. Vertical profiles of temperature by station in July 1995. Solid and dotted lines show the night (twilight) and day temperatures, respectively. Temperatures obtained from CTD in MOCNESS-I.

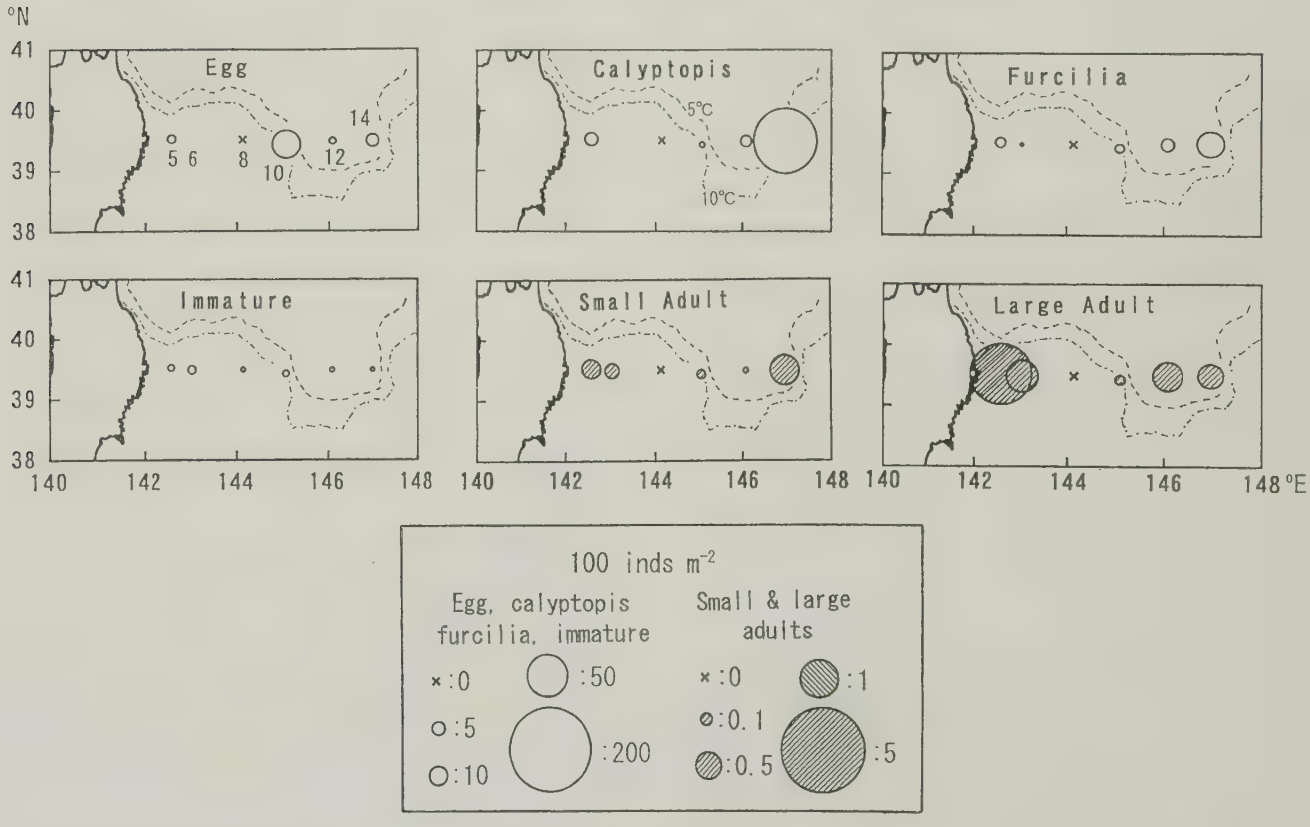

Fig. 4-15. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at night (except for St. 6 at twilight time) and temperature gradients at 100m depth in July 1995. The scales as in legend. Stations arenumbered in "egg".

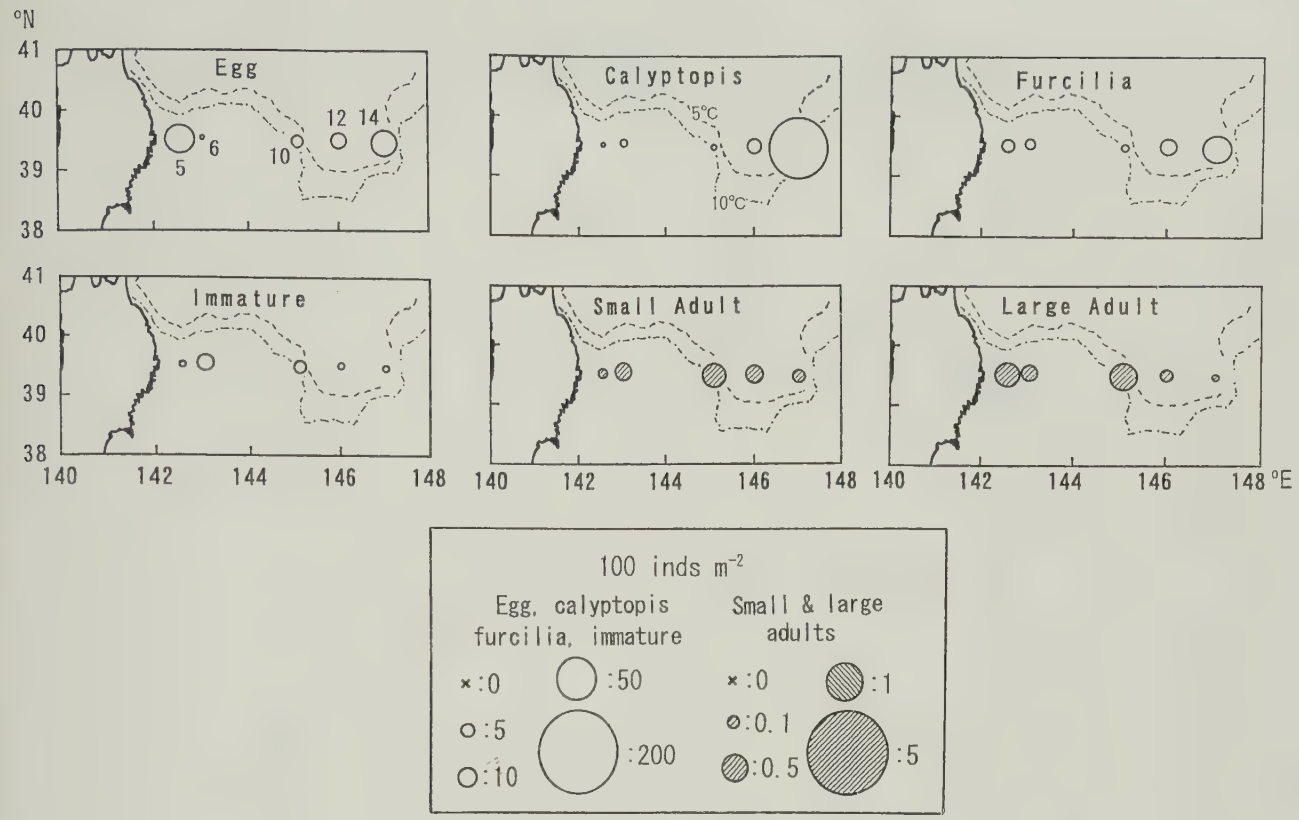

Fig. 4-16. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at day and temperature gradients at 100m depth in July 1995. The scales as in legend. Stations are numbered in "egg".

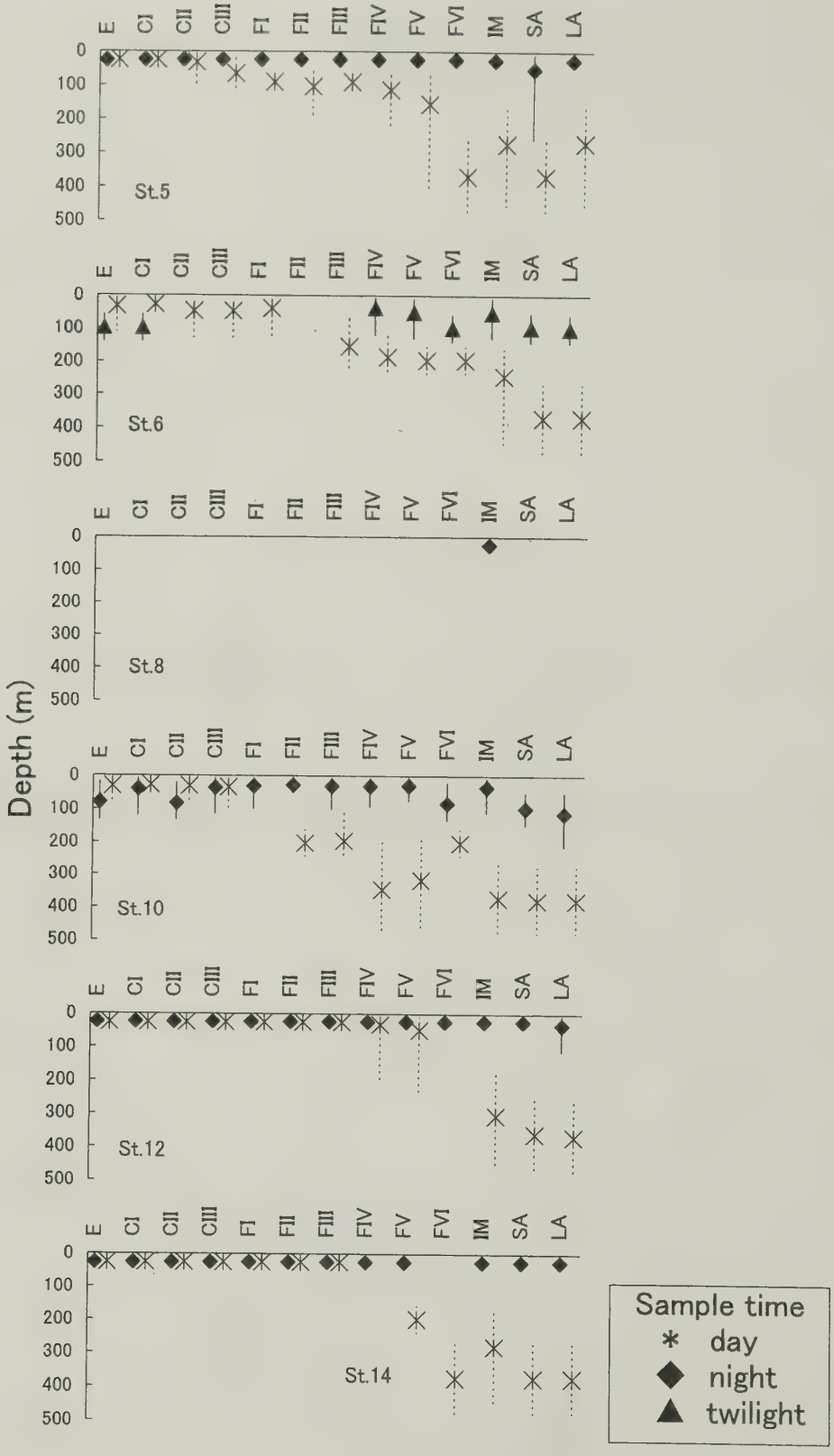

Fig. 4-17. Vertical distributions by developmental stage from egg to adult of *Euphausia pacifica* by station in July 1995. Symbols show median depth. Vertical bar shows the range of 80% of abundance. SA and LA = small (≦15mm) and large (>15mm) adult, respectively.

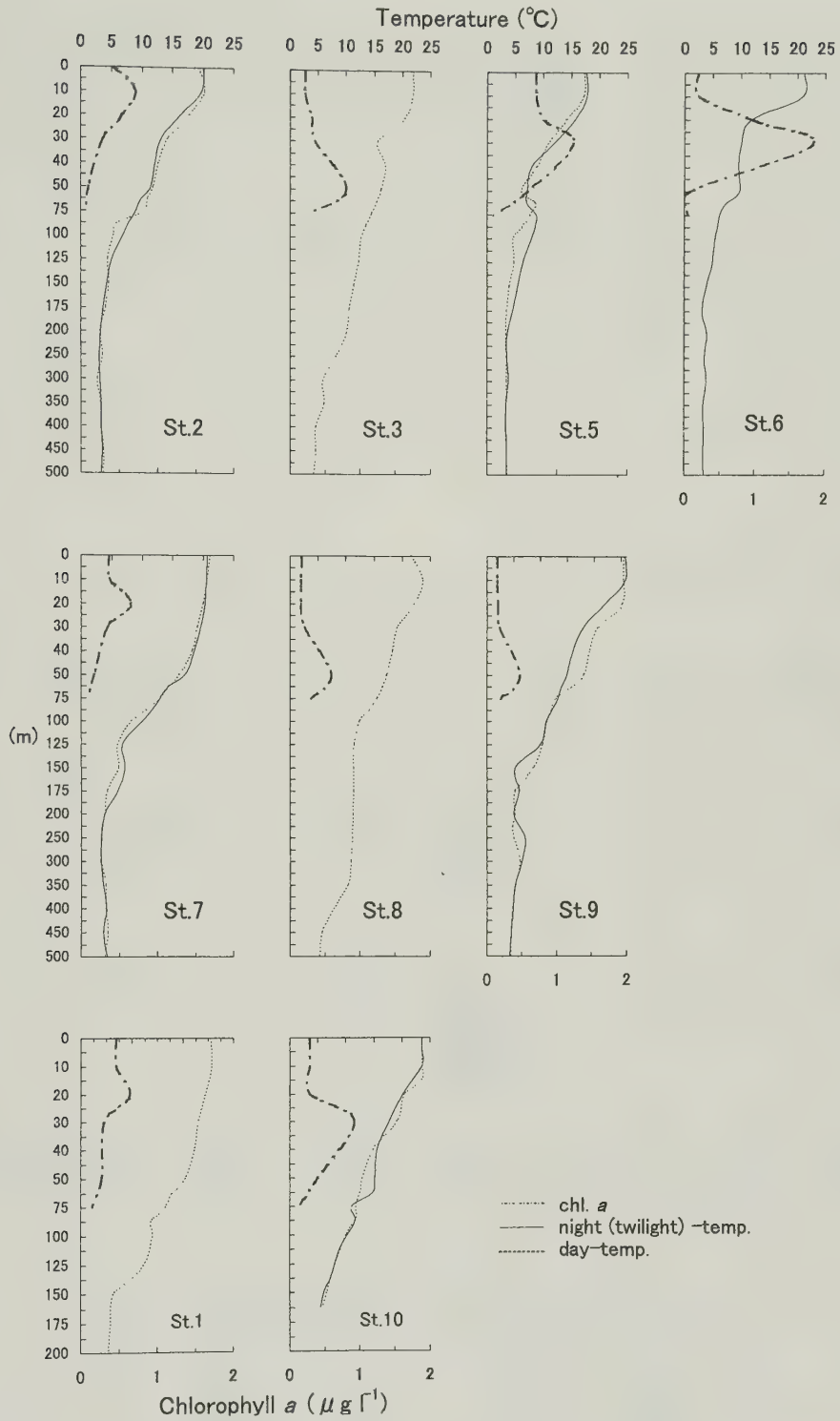

Fig. 4-18. Vertical profiles of temperature and chlorophyll *a* at each station in September 1998. Temperatures obtained from CTD in MOCNESS-I.

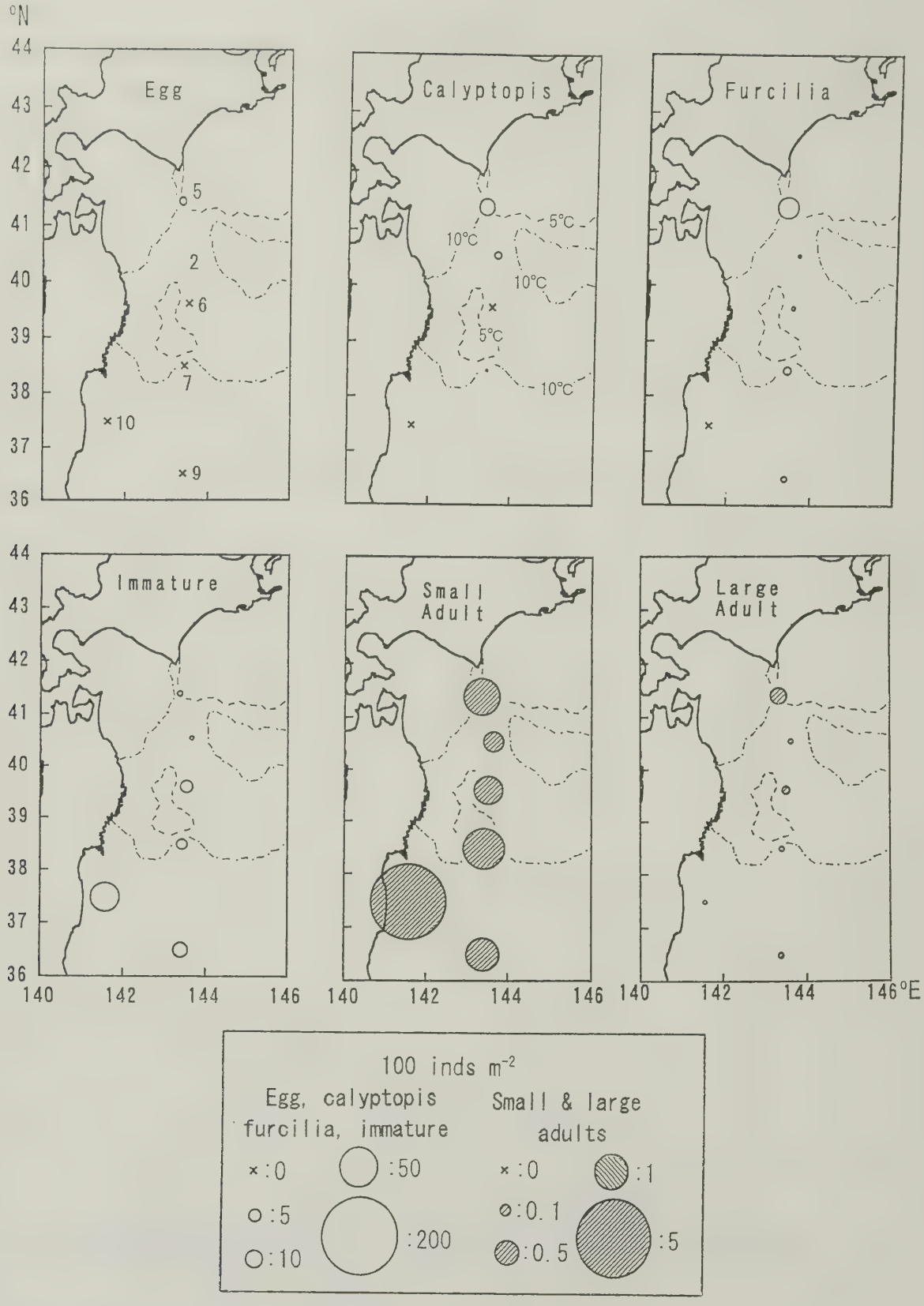

Fig. 4-19. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at night (except for St. 2, 10 at twilight time) and temperature gradients at 100m depth in September 1998. The scales as in legend. Stations are numbered in "egg".

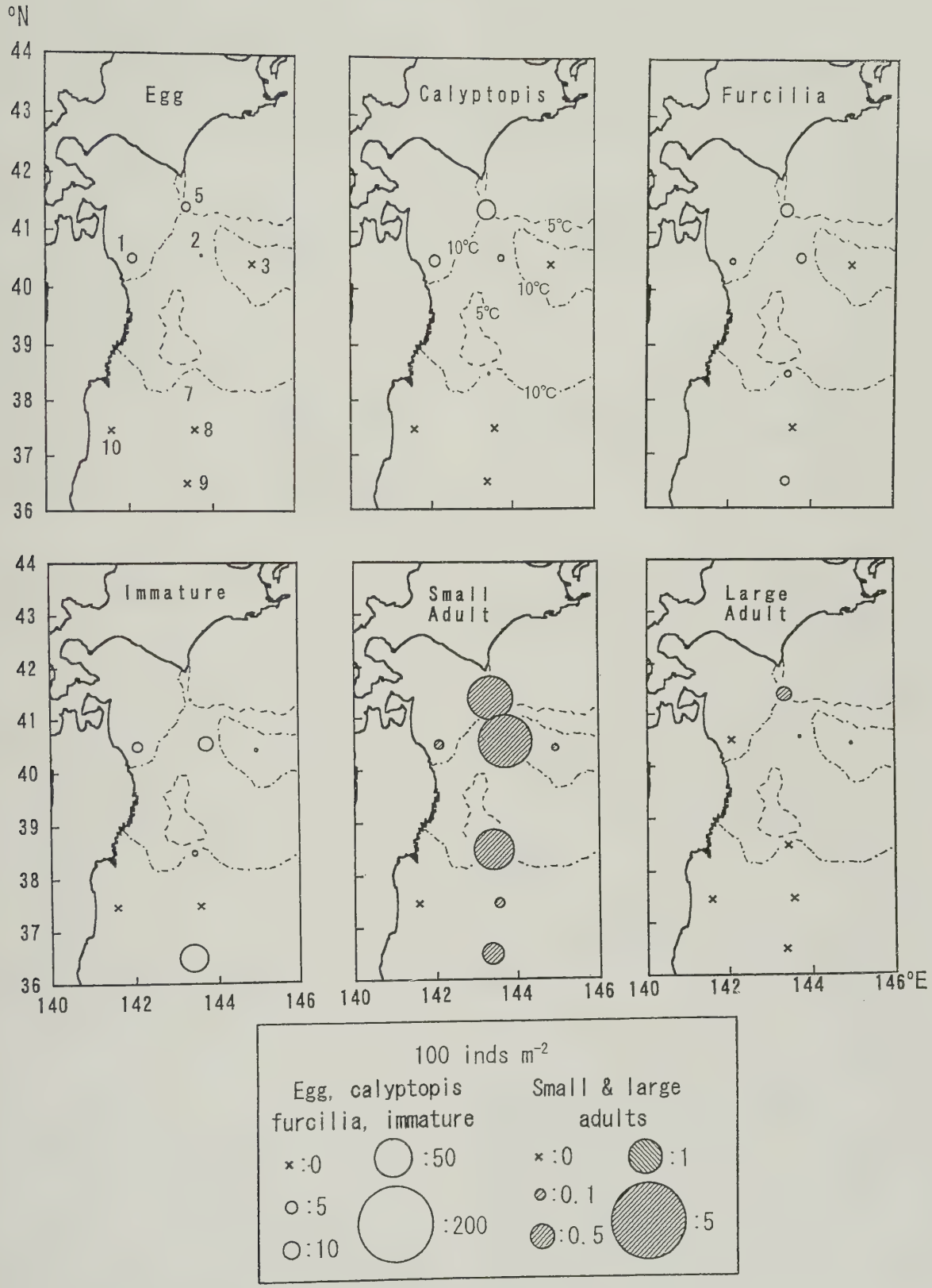

Fig. 4-20. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at day and temperature gradients at 100m depth in September. The scales as in legend. Stations are numbered in "egg".

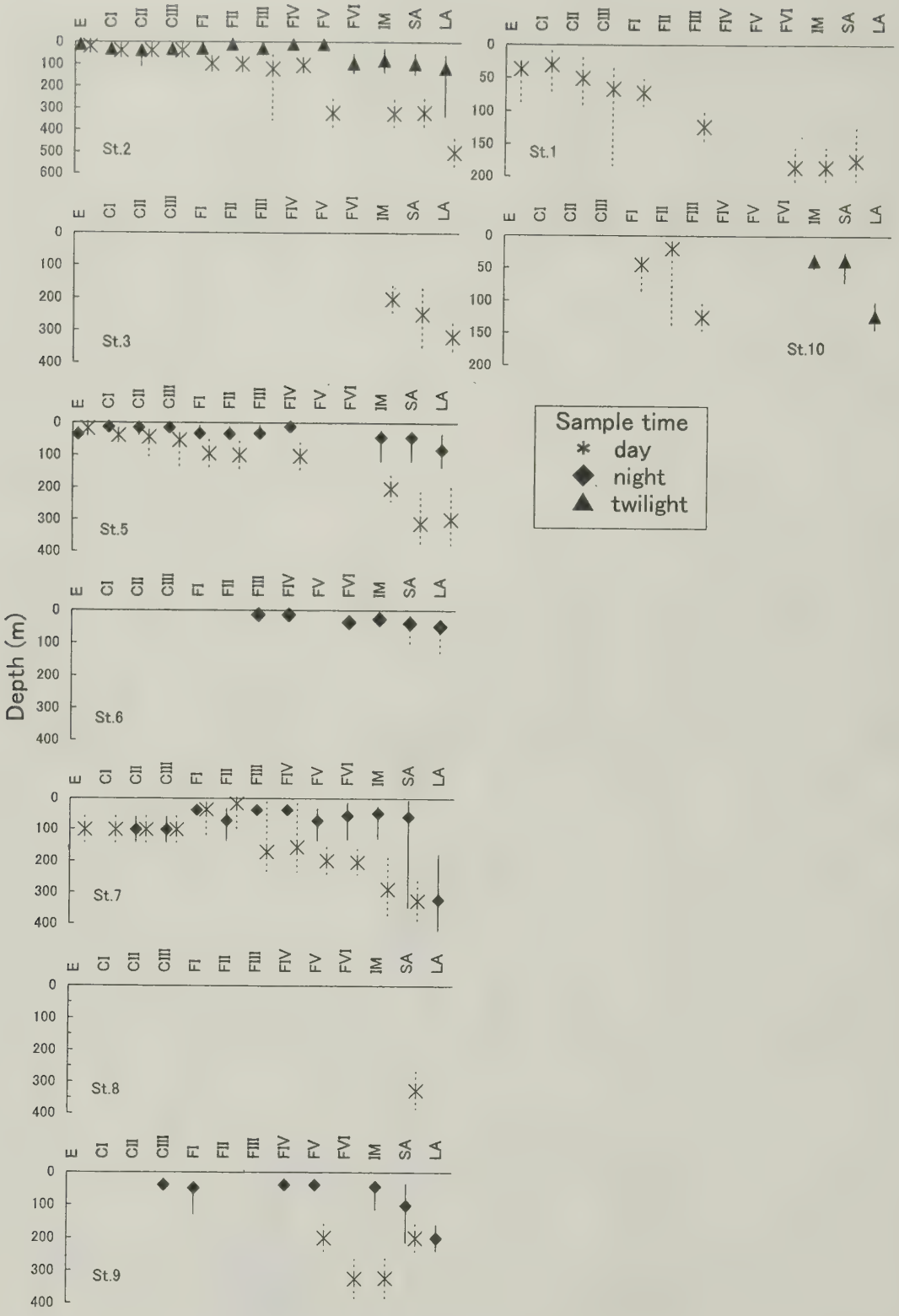

Fig. 4-21. Vertical distributions by developmental stage from egg to adult of *Euphausia pacifica* by station in September1998. Symbols show median depth. Vertical bar shows the range of 80% of abundance. SA and LA = small (≦15mm) and large (>15mm) adult, respectively.

Calyptopis and furcilia stages were abundant at St. 14 at night. Immature stage was abundant at Sts. 6 and 10 during daytime. Small adults were abundant at St. 10 during daytime and St. 14 at night. Large adults were abundant at St. 5 at night. Only immature euphausiids occurred at St. 8.

The median depth of each developmental stage at night was generally shallower than 50m at each station (Fig. 4-17). However, the median depth of developmental stages from eggs to second calyptopis and from fourth furcilia to adults at Sts. 6 and 10 at night was about 100m. The median depth of euphausiids during daytime increased with the developmental stages from calyptopis or early stages of furcilia at Sts. 5, 6 and 10. However, the depth increased with the developmental stages from fourth or fifth furcilia and younger stages stayed in the shallow layer even during daytime at Sts. 12 and 14.

Distribution of *E. pacifica* off northeastern Japan in September

Sts. 3 and 8 were located near the center of the warm-core rings (37°30'N, 144°E and 40°20'N, 145°10'E, respectively; Kato *et al.*, 2000) and higher temperatures than 10 ℃ occurred above 200m at St. 3 and above 350m at St. 8 (Figs. 4-18-20). Sts. 7 and 9 were located along the marginal area of the warm-core rings and higher temperatures than 16 ℃ occurred above 50m at both stations. St. 5 was located between the first branch of the Oyashio Current and Tsugaru Warm Current. St. 6 was located on the east side of the cold-core ring. Lower temperatures than 10℃ occurred below 30m at Sts. 5 and 6. St. 2 was located between warmer and colder water masses. St. 1 was strongly affected by the Tsugaru Warm Current (Kato *et al.*, 2000). St. 10 was located south of 10℃ isotherm at 100m depth and water with about 23℃ occurred above 20m at this station. Maximum chlorophyll *a* concentration occurred below the thermocline (generally at 30–50m) at each station except Sts. 2 and 7. Higher than 1 μ g l^{-1} occurred at 30m at Sts. 5 and 6, but maximum concentration was lower than 1 μ g l^{-1} at other stations.

A few eggs occurred at Sts. 1 and 5 but rarely occurred at other stations (Figs. 4-19 and 20). A few larvae of calyptopis and furcilia occurred at St. 5 but rarely occurred at the other stations. Immature stage and small adults occurred widely and were most abundant at St. 10 at night. Large adults occurred mainly at St. 5 at night, but rarely occurred at other stations. Every developmental stage rarely occurred at Sts. 3 and 8.

In the offshore areas, median depth of *E. pacifica* at night tended to increase with the developmental stages from fifth furcilia or immature stage at each station (Fig. 4-21). Especially, median depth of large adults was significantly deep at St. 7 (323m) and St. 9 (201m), and upper limit depth of their 80% abundance occurred below the thermocline at both stations. Median depth of euphausiid during daytime tended to increase with the developmental stages from first-third furcilia. Median depth of adults during daytime was generally about 300m at each station, but that of large adults was 501m at St. 2 and that of small adults was 200m at St. 9.

At St. 1, median depth of *E. pacifica* during daytime tended to increase with the developmental stages from second calyptopis and immature and adult stages occurred in the benthopelagic layer (Fig. 4-21). Median depth of large adults (124m) at night was deeper than that of immature and small adults (39 m) at St. 10. Immature and adult stages did not occur during daytime at St. 10.

Distribution of *E. pacifica* off northeastern Japan in November

Sts. 2 and 4 were located under the influence of the Kuroshio Extension, and higher temperatures than 15℃ occurred above 150m at St. 2 and above 200m at St. 4 (Figs. 4-22-24). Sts. 5 and 6 were located along the marginal area of the cold-core ring. Thermocline occurred between 75 and 150m at St. 5 where the temperatures were about 13℃ above 75m and about 3 ℃ below 150m. Apparent thermocline did not occurred at St. 6. St. 8 was located under the influence of the Oyashio Current and had a thermocline between 50 and 100m with lower temperature than 4℃ below 100m. Chlorophyll *a* concentration tended to be higher in the northern stations and showed 0.7～0.9 μ g l^{-1} between the surface and 50m at St. 8.

Eggs, calyptopis and furcilia stages occurred limitedly along the marginal area of the cold-core ring and were most abundant at St. 5 (Figs. 4-23 and 24).

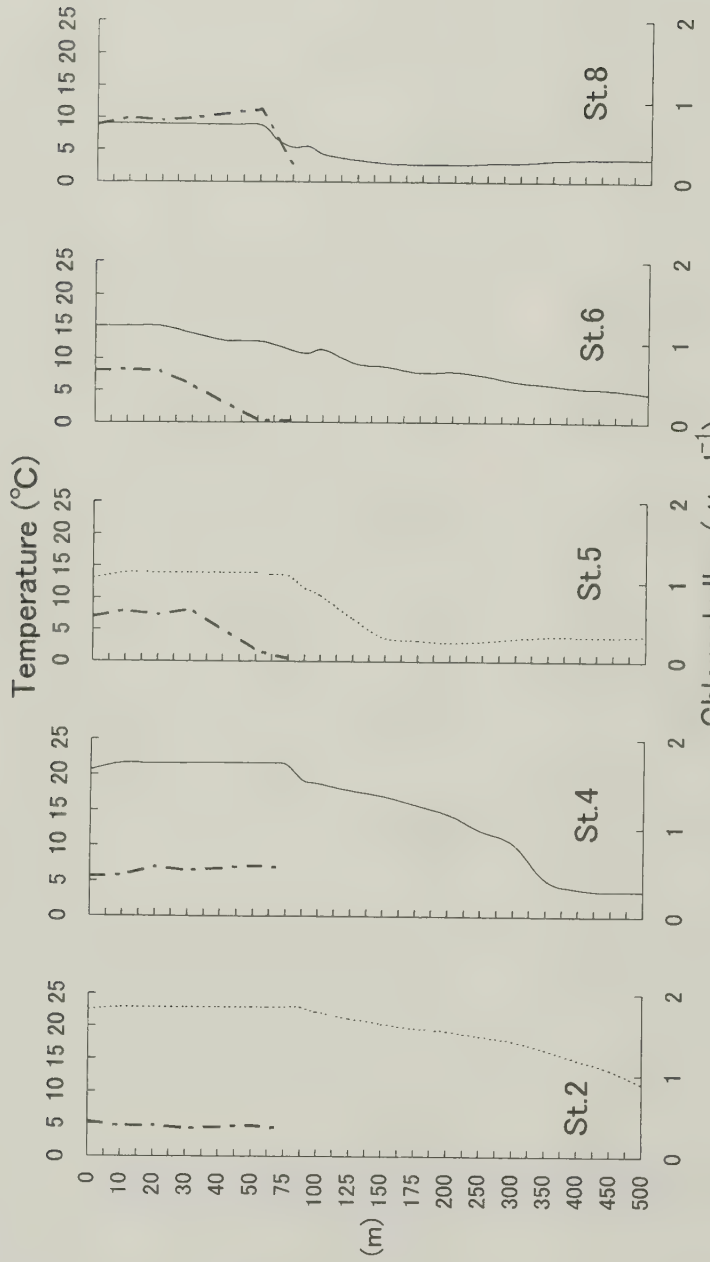

Fig. 4-22. Vertical profiles of temperature and chlorophyll *a* at each station in November 1999. Temperatures obtained from CTD in MOCNESS-I.

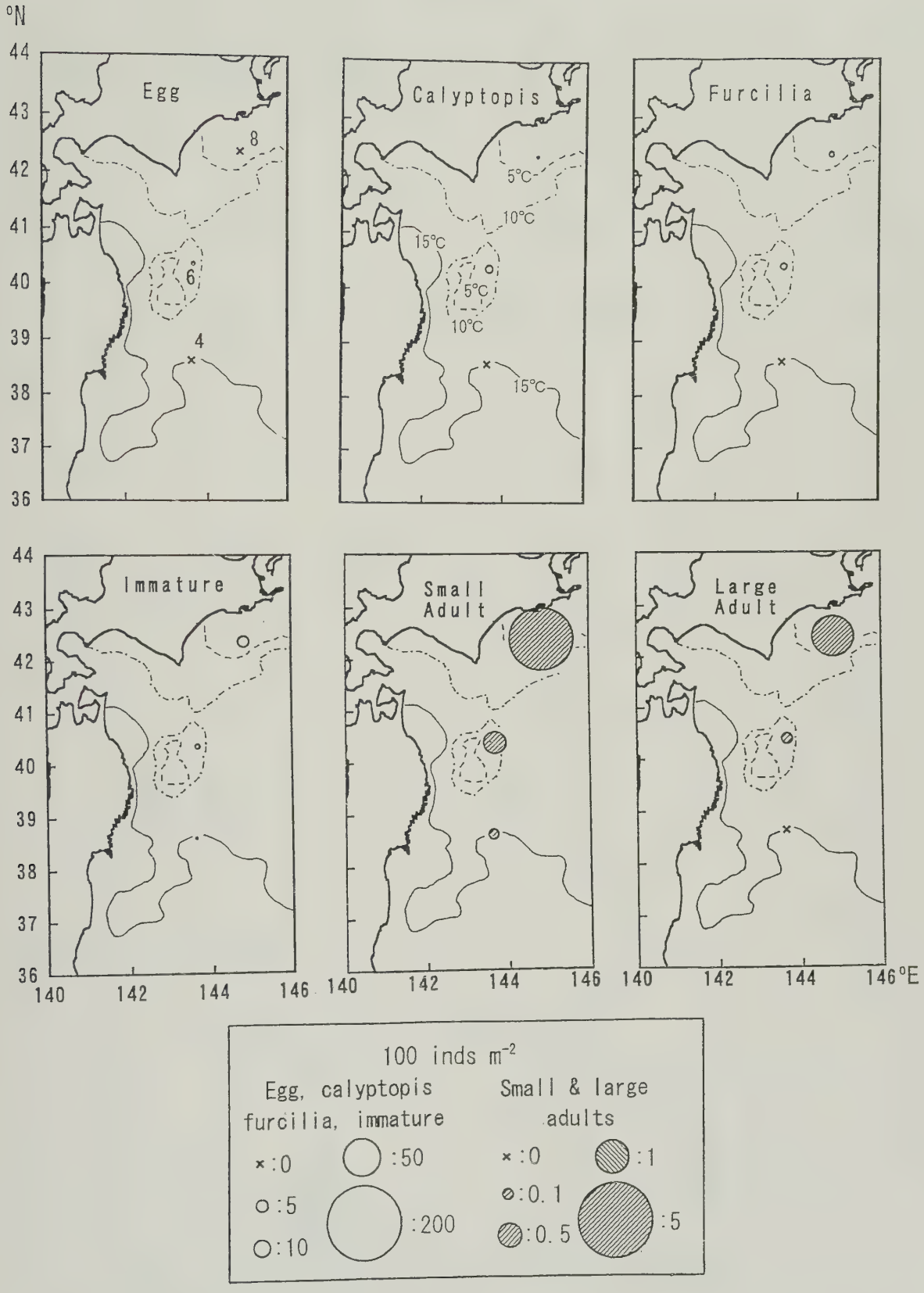

Fig. 4-23. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at night and temperature gradients at 100m depth in November. The scales as in legend. Stations are numbered in "egg".

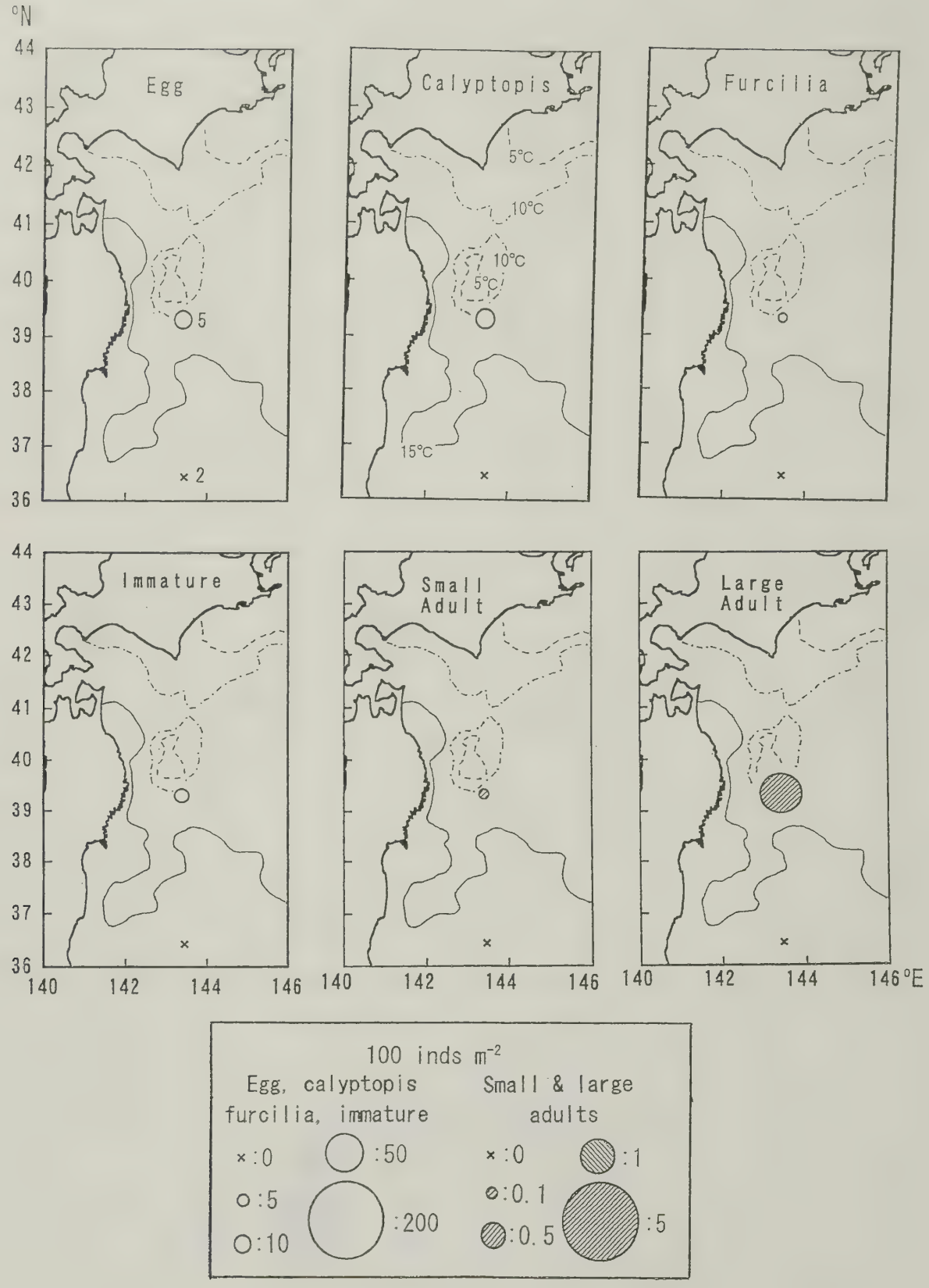

Fig. 4-24. Distribution and abundance of each developmental stage of *Euphausia pacifica* collected at day and temperature gradients at 100m depth in November. The scales as in legend. Stations are numbered in "egg".

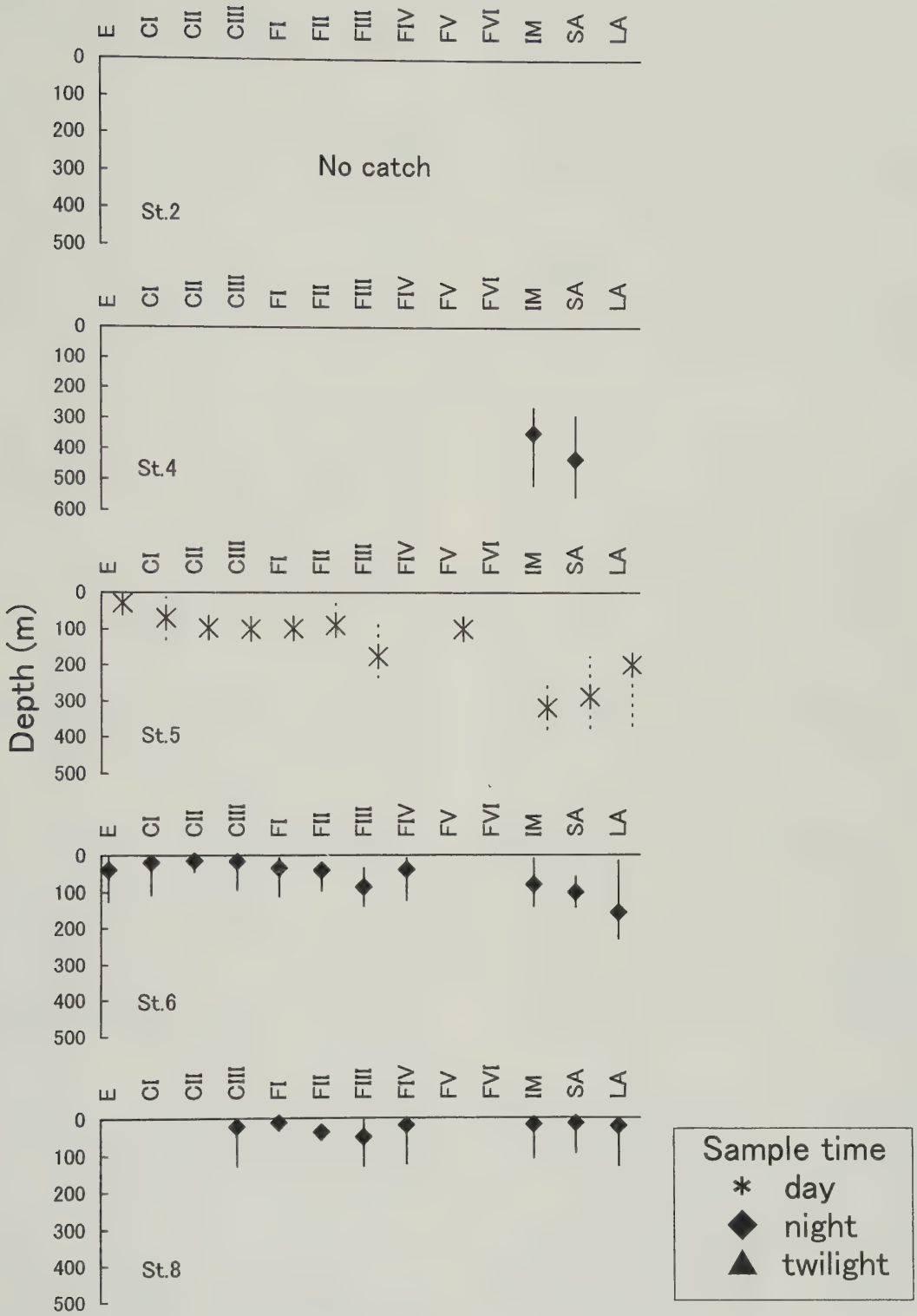

Fig. 4-25. Vertical distributions by developmental stage from egg to adult of *Euphausia pacifica* by station in November 1999. Symbols show median depth. Vertical bar shows the range of 80% of abundance. SA and LA = small (≦15mm) and large (> 15mm) adult, respectively.

Immature stage occurred at Sts. 5 and 8. Small and large adults were abundant at St. 8. Every developmental stage rarely occurred at Sts. 2 and 4.

Median depth of each developmental stage at night was shallower than 50m at St. 8 (Fig. 4-25). Median depths of *E. pacifica* at night increased with the developmental stages from immature stage and that of large adult was 232m at St. 6. Median depth of immature and small adults at night was significantly deeper (436m each) and upper limit depth of 80% abundance occurred at 267 and 294m, respectively, which were slightly shallower than the thermocline (300-350m).

Discussion

Characteristics of the pelagic and benthopelagic *E. pacifica* in the Sanriku coastal waters

From the ORI and beam-trawl net surveys, immature and adult *E. pacifica* seem to be distributed mainly on the upper slope where cold temperatures ≦8℃ occurred in the near bottom layer, forming a benthopelagic population from early summer to fall in the Sanriku coastal waters (Figs. 4-3-9). On the other hand, adult *E. pacifica* seems to form dense aggregations above the continental shelf where water with 7-8℃ dominates in the total water column and are pelagic throughout the day in spring (Figs. 4-3-9). MOCNESS-I net survey in the coastal waters in spring supported the latter conclusion, i.e. adults occurred mainly above 100m at St. 15 both during day and night in April (Fig. 4-13). On the other hand, immature and adult *E. pacifica* did not occur in the total column during day although they occurred abundantly at night at St. 10 in September (Figs. 4-19-21). Endo (2000) observed that benthopelagic *E. pacifica* aggregations occurred in the sea depth range from 160-400m off Sanriku in summer and their thickness was a few meters from the sea bed. Therefore no collection of immature and adult stages during day at St. 10 may be due to sampling failure of the benthopelagic *E. pacifica* by MOCNESS-I net of which deepest tow depth was ca. 30 m above the sea bed.

Greene *et al.* (1988) suggested that *Meganyctiphanes norvegica* reaches the sea bed and forms benthopelagic aggregations in coastal waters during day at depths less than the usual diurnal vertical migration in the offshore waters. Daytime depth (300-400m) in the offshore waters in summer and fall seems to cause the formation of benthopelagic population on the upper slope for *E. pacifica*. On the other hand, adults were abundantly collected by beam-trawl net even at night in October and December (Fig. 4-7). This may be due to 1) contaminated sampling with pelagic *E. pacifica* during the retrieval of the net from the sea bed to the surface or 2) the collection of genuine benthopelagic population at night because the occurrence of the thermocline in the middle-deeper layer prevented *E. pacifica* from ascending toward the upper layer as observed in the warm offshore waters (Figs. 4-21 and 25). A trawl net survey using a closing net mechanism is necessary to confirm the accurate time of formation of benthopelagic aggregations.

Benthopelagic *E. pacifica* on the upper shelf was most abundant in June. This was perhaps originated from 1) the active recruitment of the spring-hatched cohort because recruitment time from hatching to immature or adult stages takes ca. 2 months (e.g. Endo, 1981) and 2) abundant overwintered individuals which formed dense pelagic populations in the Sanriku waters in spring.

The trophic significance of *E. pacifica* in the Sanriku coastal waters is suggested from the results of the present study as follows. In spring, *E. pacifica* plays an important role as food for plankton-feeding fishes living in the shallow waters such as sand lance and sea-birds such as *Aethia cristatella* and *Cerorhinca monocerata* (Odate, 1991), because it forms dense aggregations in the shallow layers on the continental shelf during day. On the other hand, from early summer to fall, *E. pacifica* plays an important role as food for demersal fishes such as walleye pollack, because it forms a benthopelagic population on the upper slope. Fujita (1994) showed that demersal fishes in the coastal waters off Otsuchi, Iwate Prefecture and off Sendai Bay, Miyagi Prefecture ingested *E. pacifica* most actively from May to July. In the present study, benthopelagic *E. pacifica* on the upper shelf was most abundant in June. So, demersal fishes seem to make the most of benthopelagic *E. pacifica* as food in early summer when it is most abundant. The abundance of *E. pacifica* in ear-

ly summer may have a strong effect on the life history of these demersal fishes.

Joint samples of plankton and predators are necessary to further quantify these relationships.

Characteristics of seasonal horizontal distribution in the offshore waters

There are apparently three tendencies in the horizontal distribution in the offshore waters as follows. 1) Eggs and larval stages were most abundant in the transitional area off Sanriku and Joban in April but rarely occurred in the Oyashio area off southern Hokkaido in the same months (Figs. 4-11 and 12). 2) Small adults occurred widely in the Oyashio and transitional areas in each month although large adults rarely occurred in the warmer waters of the transitional area ($10℃ < T_{100} \leqq 15℃$; Figs. 4-19 and 20). 3) Every developmental stage rarely occurred in the Kuroshio area (Figs. 4-23 and 24). These evidences are consistent well with the results obtained by the horizontal distribution survey in Chapter 3.

Diurnal vertical migration of each developmental stage

Euphausiid eggs are generally thought to have a higher specific gravity than sea water and sink after liberation from gravid female (Mauchline and Fisher, 1969) but eggs of *E. pacifica* seem to be rather neutral because they were generally distributed within 100m or so in vertical range (Figs. 4-13, 17, 21 and 25).

Annual average median depth of each developmental stage of *E. pacifica* during day and night for all offshore stations in the MOCNESS-I net survey is shown in Fig. 4-26. The average median depth at night was shallower in eggs, calyptopis and early and middle stages of furcilia and tended to increase with the developmental stages from middle stages of furcilia to large adults, while that during day was shallowest in eggs and first calyptopis and tended to increase with developmental stages from first calyptopis to sixth furcilia. Gradual extension of the vertical range with developmental stages is well consistent with the trend reported in other populations (Brinton, 1967; Bollens *et al.*, 1992; Iguchi, 1995).

Annual average water temperature at the median depth of each developmental stage during day and night is shown in Fig. 4-27. The average water temperature at night was highest at about 12 ℃ in calyptopis and furcilia stages, and was 9.8, 10.2, 9.0, 8.0 ℃ in eggs, immature and small and large adults, respectively, while that during day was highest of 9.2, 11.2℃ in eggs and first calyptopis, respectively, and gradually decreased with the developmental stages from first calyptopis to immature (ca. 4℃). The change in pattern with developmental stages at night is well consistent with both that for the horizontal distribution by water mass (Table 3-2) and that for the vertical distribution (Fig. 4-26). This suggests that the vertical distribution at night of each developmental stage relates closely to the respective suitable temperatures. On the other hand, the change in pattern with developmental stages during day is well consistent with that for the verti-

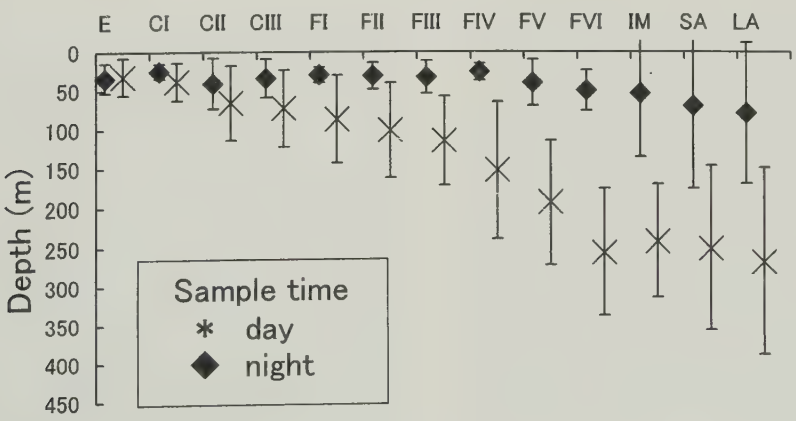

Fig. 4-26. Average vertical distribution by development stage from egg to adult of *Euphausia pacifica* for offshore stations in July 1995, April and September 1998, and November 1999. Symbols show the average median depth. Vertical bar shows standard deviation.

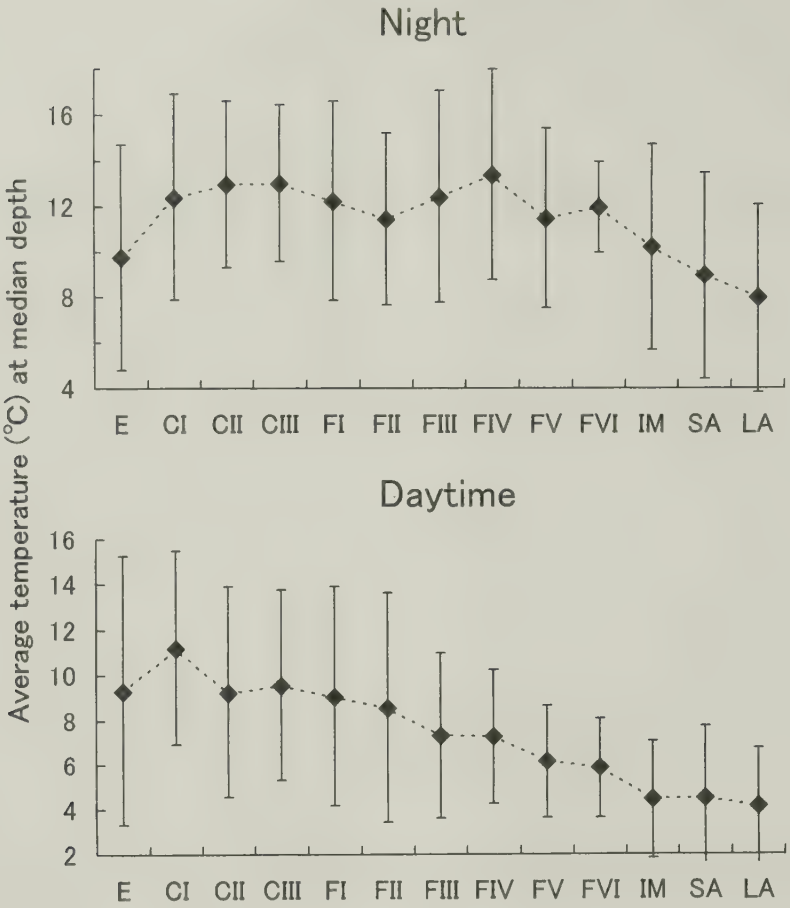

Fig. 4-27. Average water temperature at the median depth of each developmental stage of *Euphausia pacifica* for offshore stations in July 1995, April and September 1998, and November 1999. Vertical bar shows standard deviation.

cal distribution (Fig. 4-26). The vertical distribution of each developmental stage during day is thought to be related to not only the suitable temperatures but also swimming ability because larval stages are generally considered to take place diurnal vertical migration in the shallower layer in order to effectively utilize phytoplankton in the surface layer due to their weak swimming ability (Mauchline and Fisher, 1969; Iguchi, 1995). However, the reason why pre-third furcilia stages stayed in the surface layer even during daytime in the Oyashio area in July seems to be due to avoidance of cold temperatures of <4 ℃ that occurred below the thermocline and acceleration of growth in the warm surface layer (see Ross, 1981).

Median depth of *E. pacifica* both during day and night tended to be deepest in eggs or calyptopis and become shallow with the developmental stages from calyptopis to advanced stages at coastal stations in April, which was quite different from the diurnal vertical migration pattern with developmental stages usually found at the offshore stations (Fig. 4-13). According to Nakagawa *et al.* (2001), adult *E. pacifica* can ingest copepods with prosome length of 2.1mm which almost equals to the total length of the third calyptopis. Therefore, it is suggested that copulated females liberate their eggs in the deeper layers and larval stages avoided adults by controlling their diurnal vertical migration to minimize cannibalism by the adults abundantly distributed in the surface layer. A change in diurnal vertical migration pattern of furcilia stage in *E. pacifica* according to the abundance of predators was also observed in Dabob Bay, off western USA (Bollens *et al.*, 1992).

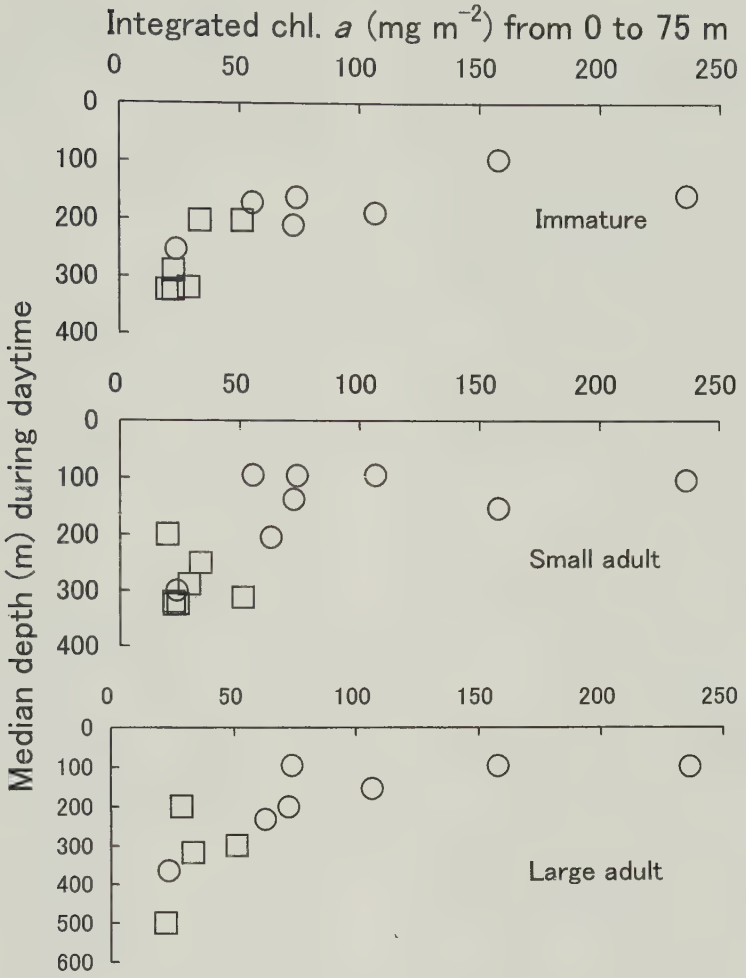

Fig. 4-28. Relationship between median depth during daytime of immature, small and large adult *Euphausia pacifica* for offshore stations and the integrated concentration (mg m^{-2}) of chlorophyll *a* from 0 to 75m depth. Circle: station in April 1998, square: station in July 1995, September 1998 and November 1999.

Characteristics of diurnal vertical migration of immature and adult stages

Iguchi *et al.* (1993) suggested that post larval stages of *E. pacifica* avoid ascending into the surface high temperatures at night during summer and fall in Toyama Bay. The results of Iguchi *et al.* (1993) seems to be consistent with the present study; i.e. median depth at night of immature and adult stages tended to be deeper in the warmer areas in summer and fall, especially large adults hardly reached beyond the thermocline in the mid layer (Figs. 4-21 and 25). However, median depth at night of adults at St. 6 in November was significantly deeper than that at St. 1 in April, although the vertical distribution of water temperatures was similar between the two stations (Figs. 4-10, 13, 22 and 25). Therefore, seasonal difference in nighttime depth of adult *E. pacifica* may be due to not only temperatures but also other factors such as seasonal food conditions because adult *E. pacifica* tends to ingest diatoms positively when they are abundant in the surface layer as mentioned later in Chapter 6.

Endo (1981) suggested that adult *E. pacifica* needs not to descend to deeper layers in the colder regions because it can reduce metabolic expenditure in the shallow cold layers, while it needs to descend to the deeper layers below the thermocline in

the warmer regions, referring to the hypothesis by McLaren (1963). Endo's results seems to be consistent with the present ones, i.e. median depth during daytime of immature and adult stages in April, where the thermocline did not develop, was significantly shallower ($P < 0.01$; Mann-Whitney) than that in other months and thus distance of diurnal vertical migration tended to be shorter in April (Fig. 4-13). However, median depth during daytime of large adults was shallow (97m) at St. 2 where the surface temperature was higher than 15℃, while that was quite deep (326) m at St. 9 where temperatures lower than 3℃ dominated in the total water column (Fig. 4-13). In addition, median depth during daytime of immature and adult stages was quite deep (250-500m) in spite of the occurrence of a thermocline above 50m depth at St. 14 in July (Fig. 4-17). On the other hand, median depth during daytime of immature and adult stages at the offshore stations where the concentration of chlorophyll *a* from 0 to 75m was higher than 50mg m^{-2} was significantly shallower ($P < 0.05$; Mann-Whitney) than that where concentration was lower than 50mg m^{-2} (Fig. 4-28). Therefore, it is suggested that the median depth during daytime depends not only vertical distribution of temperatures but also on the illumination caused by the density of phytoplankton which could affect the vulnerability to visual predators in the shallow layer.

Chapter 5. Biomass, production and metabolism of *Euphausia pacifica*

Euphausia pacifica is an important fisheries resource and food item for many fishes off the northeastern Pacific coast, and their biomass and production has been actively studied (Brinton and Reid, 1986; Gomez-Gutierrez and Robinson, 1997; Heath, 1977; Tanasichuk, 1998a). Off the Japanese coast, biomass and production of the species have been studied only in Toyama Bay, Japan Sea (Iguchi and Ikeda, 1999), but such studies have not yet been conducted off the Pacific coast of northeastern Japan.

In this chapter, biomass, production (growth, eggs, moults) and metabolism (routine and diurnal vertical migration) of *E. pacifica* were investigated along the coastal waters off northeastern Japan, and characteristics of carbon budgets of *E. pacifica* off northeastern Japan are discussed comparing with the same species from other regions as well as other euphausiid species.

Materials and Methods

The analyses of biomass and production of *Euphausia pacifica* were based on bimonthly samples collected using Norpac nets (diameter: 0.45m; mesh size: 0.34mm) and 5.5m long cylindrical-conical nets (diameter: 1.3m; mesh size: 0.45mm; Watanabe, 1992) along the coastal waters off southeastern Hokkaido (41°-43°N), Sanriku (38°-41°N) and Joban (36°-38°N) on the R. V. *Wakataka-maru* (Tohoku National Fisheries Research Institute, Fisheries Research Agency), *Tankai-maru* and *Hokko-maru* (Hokkaido National Fisheries Research Institute, Fisheries Research Agency) from March 1997 to February 1998. The March survey was conducted only off Sanriku. The abundance of eggs and calyptopis stage (ca. <1 to 2mm body length) was determined from the Norpac net collections, those of furcilia (ca. > 2 to 6mm), immature (ca. >6 to 10mm) and adult (ca. >10mm) stages were determined from the cylindrical-conical net collections. Norpac nets were vertically towed from 150m to the surface at 1m s^{-1}. The cylindrical-conical nets were obliquely towed at a ship speed of 2 knots from 15m above the sea bottom to 0m where the sea depth was shallower than 300m, and towed from 150 to 0m where the sea depth was deeper than 300m. Cylindrical-conical net was towed only at night at all stations because postcalyptopis stages migrate below the 150m depth in the daytime, but mostly occur at < 150m depth at night (see **Chapter 4**), except at stations along the zigzag acoustic survey lines between 100 and 300m isobaths off Sanriku and Joban in March and April (Miyashita *et al.*, 1998). Water temperature and salinity from 0 to 300m depth were measured by CTD (Sea-Bird). More details on sampling methods, the results of seasonal changes in oceanographic features and the distribution and spawning activity of *E. pacifica* using the same samples can be found in **Chapter 3**.

The body length (BL: the distance between the tip of the rostrum and distal end of the telson) was

divided into 1mm increments (24 size classes over the entire range of <1 to 24mm BL). The relationship between BL (mm) and dry weight (DW) for *E. pacifica* was calculated as $DW = 9.954 \times 10^{-4} BL^{3.156}$, according to Iguchi and Ikeda (Iguchi and Ikeda, 1995). Carbon contents of each developmental stage and size class of *E. pacifica* were calculated according to Iguchi and Ikeda (1998).

Average biomass (B) of each coastal area and entire survey area during entire survey period was calculated as

$$B = \sum_{i=1}^{S} ((B_i + B_{i+1}) \times d_{i,\,i+1}/2) \,/\, \sum d_{i,\,i+1} \quad (5.1)$$

where B_i is biomass of ith survey, $d_{i,\,i+1}$ is days between ith survey and $(i+1)$th survey. The entire study period was 313 days (six sampling periods) for the coastal areas off southeastern Hokkaido and Joban, and 356 days (seven sampling periods) for the coastal area off Sanriku. The entire study period for the entire survey area was presumed to be 356 days (seven sampling periods) on the assumption that the biomass and production off Sanriku in March 1997 stands for the average off all three coastal areas in the same month.

The somatic production of *E. pacifica* was computed as the sum of growth increments of 24 size classes multiplied by the abundance of each size class:

$$P_g = \sum_{i=1}^{S} ((CW_{i+1} - CW_i) \,/\, D_i \times N_i) \quad (5.2)$$

where P_g is the daily somatic production (mg C m^{-2} day^{-1}), i is the size class, CW_i and CW_{i+1} are carbon weight (mg C) at the beginning and end of the size interval, D_i is the developmental time (days) from CW_i to CW_{i+1}, N_i is the average abundance (ind. m^{-2}) of each size class and s is 24.

To obtain CW, BL data were converted to dry weight (DW) using the allometric equation, then to carbon units by multiplying carbon content data for each BL class mentioned above. Monthly size-frequency distribution of *E. pacifica* along the three coastal areas is shown in Fig. 5-1. *E. pacifica spawns* near the marginal area of the Oyashio Current (T_{100} = 5℃) throughout the year (see **Chapter 3**), so continual occurrence of small size individuals off Sanriku and Joban throughout the year (Fig. 5-1) may be due to transportation from the adjacent spawning area, although spawning occurs limitedly in spring in the both areas (see **Chapter 3**). Discrete cohorts are difficult to follow on the basis of such considerable overlap of small size ranges. Therefore, the growth rates of individuals for ≦10mm size classes (corresponding to larval and immature size) were estimated to be 0.1mm day^{-1} throughout the year as reported by many field studies (Heath, 1977; Bollens *et al.*, 1992; Brinton, 1976; Iguchi *et al.*, 1993; Smiles and Pearcy, 1971). The growth rates for > 10mm size classes (corresponding to adult size) were estimated from the population size-frequency distributions of adult stage over the whole coastal area using the software application (Macdonald and Green, 1988), assuming that the seasonal growth rate was common in the three coastal areas because adult *Euphausia pacifica* could migrate between coastal areas with the seasonal change of waters masses according with the Oyashio Current and may not spend its entire life history in each individual area (see **Chapter 3**).

The estimations of moult and egg production needed the assumption of habitat temperatures for each developmental stage of *E. pacifica*. The median depths of eggs and the calyptopis stage are shallower than 50 m in the Sanriku waters in both spring and summer regardless of the difference of water masses, except along the coastal waters in spring (7-8℃ dominated throughout the water column) where their median depths are deeper than 100 m (see **Chapter 4**). The median depths of the furcilia stage are at the surface layer at night and shallower than 150m during daytime in the Sanriku waters in both spring and summer regardless of the water masses. Therefore, the daily average temperature that *E. pacifica* encounters was estimated to be the average temperature from 0 to 50m for eggs and calyptopis stage and from 0 to 150m for furcilia stage for each coastal area in each month. The median depths of immature and adult stages are at the surface layer at night and about 150m during daytime in the Sanriku waters in spring (see **Chapter**

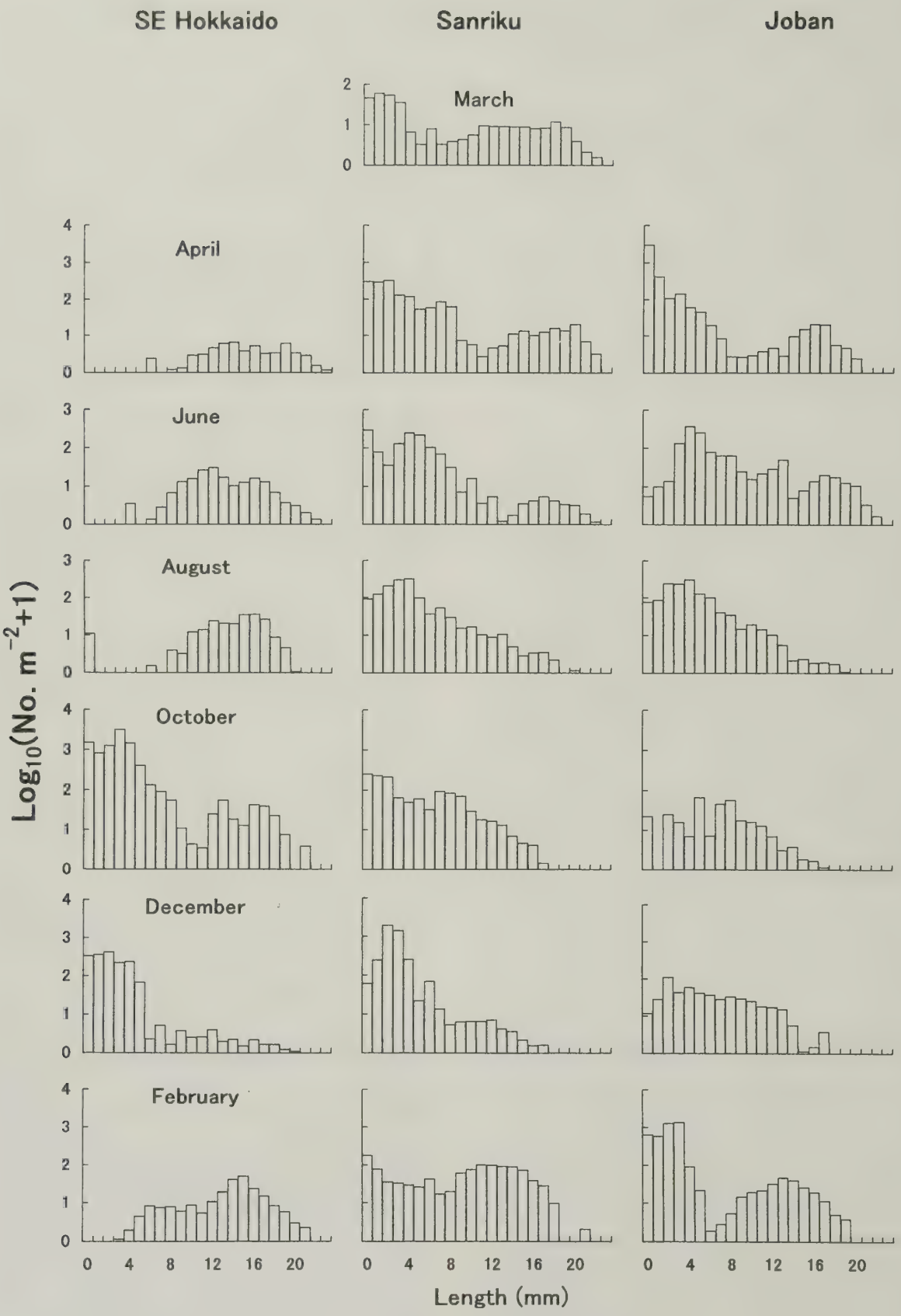

Fig. 5-1. Monthly size-frequency distribution of *Euphausia pacifica* from March 1997 to February 1998 along the three coastal areas: off southeastern Hokkaido, Sanriku and Joban.

4), therefore the daily average temperature for immature and adult stages was estimated to be the average temperature from 0 to 150m for each coastal area in March, April 1997 and February 1998. In summer, their median depths during daytime are about 300m, and those depths at night are deeper than the surface layer due to avoidance of high surface temperatures (see **Chapter 4**). The average temperature at the upper limit depth of $D_{80\%}$ (80% range of abundance from the median depth; Pennak, 1943) at night in summer was 17.4, 14.8 and 9.9℃ for immature stage, small adults (≦ 15mm) and large adults (>15mm), respectively. Therefore, the daily average temperature was estimated to be the average temperature from the depth of 17℃ to 300m for immature stage, from the depth of 15℃ to 300m for small adults and from the depth of 10℃ to 300m for large adults during June-December 1997.

The production of moults is given by the equation:

$$P_e = \sum_{i=1}^{S} (a \times DW_i \times N_i) / IP_i \quad (5.3)$$

where P_e is the moult production (mg C m^{-2} day^{-1}), DW_i is the dry weight of each size class, N_i is the average abundance of each size class, a is the percent loss in body DW per moulting (4.0%; Iguchi and Ikeda, 1999) multiplied by carbon content of moults (23% of dry weight; Iguchi and Ikeda, 1998), and IP_i is the intermoult period (days) of immatures and adults (>6mm) estimated from $\log_{10} IP_i = 0.321BL + 10^{0.034-0.0435T}$, where T is in ℃ (Iguchi and Ikeda, 1995).

The production of eggs was computed by the equation:

$$P_r = E \times CW_e / D_e \quad (5.4)$$

where P_r is the egg production (mg C m^{-2} day^{-1}), E is the average abundance of eggs (number m^{-2}), De is the average hatching time calculated from De = $8.0925 \times e^{-0.1389T}$ [estimated from the relationship between hatching times and temperatures (Table 1 in Iguchi and Ikeda, 1994)] and CWe is the carbon weight of an egg (2.4 μg C; Iguchi and Ikeda, 1998).

The metabolism (M; mg C m^{-2} day^{-1}) was partitioned into two components; routine metabolism (M_{rtn}) and diurnal vertical migration metabolism (M_{div}) developed by Iguchi and Ikeda (1999). M_{rtn} was represented by the mean routine oxygen consumption rate (R: μl O_2 $indiv.^{-1}$ hr^{-1}) of *E. pacifica* placed in a pressurized (40 atm) and unpressurized (1 atm) annular respirometer by Torres and Childress (1983), combined with the body exponent (0.85) of oxygen consumption rates obtained for an allied species *E. superba* by Ikeda (1984), i. e. $R = a\,DW^{0.85}$. a = 1.03 at 8℃ (Torres and Childress, 1983). M_{div} is the amount of oxygen consumed in the diurnal vertical migration (R': μl O_2 $indiv.^{-1}$ km^{-1}), which was calculated from the equation of net cost of transport as a function of weight (mg DW) of animals established for pelagic crustaceans ("multiple-paddle" propulsive system as compared with "undulatory" propulsion system of fish): $R' = 28.74\,DW^{0.72}$ (Torres, 1984; the original equation based on energy units was modified using the oxycalorific equivalent of 1 cal = 208.33 μl O_2 and water content of *E. pacifica* (80%) by Iguchi and Ikeda (1999)). R' is independent of temperature in theory (cf. Morris *et al.*, 1990). Thus, each metabolism is given by equation:

$$M_{rtn} = a \times 24 \times 10^{-3} \times b \times \sum DW_i^{0.85} \times N_i \quad (5.5)$$

$$M_{div} = d \times 10^{-3} \times 28.74 \times b \times \sum DW_i^{0.72} \times N_i \quad (5.6)$$

where a (1.03 at 8℃) for each habitat temperature mentioned above is computed using the mean Q_{10} = 2.1 obtained in the experiment of Torres and Childress (1983), b (0.97 × 12/22.4) is conversion factor for oxygen (volume) to carbon (weight) assuming protein metabolism (RQ = 0.97; Gnaiger, 1983), DW_i is the dry weight of each size class, N_i is the average abundance of each size class, d is diurnal vertical migration distance (km) defined as above.

The carbon assimilated by *E. pacifica* (A; mg C m^{-2} day^{-1}) is defined as $A = P + M = P_g + P_e + P_r + M_{rtn} + M_{div}$, assuming no leakage of soluble organic matter from the body. The amount of ingested carbon (I: mg C m^{-2} day^{-1}) was computed by adopting an assimilation efficiency value of 84 % determined on *E. pacifica* by Lasker (1966), i.e. $I = A/0.84$.

Each production and metabolism (PM) of each coastal area and entire survey area during entire survey period was calculated as

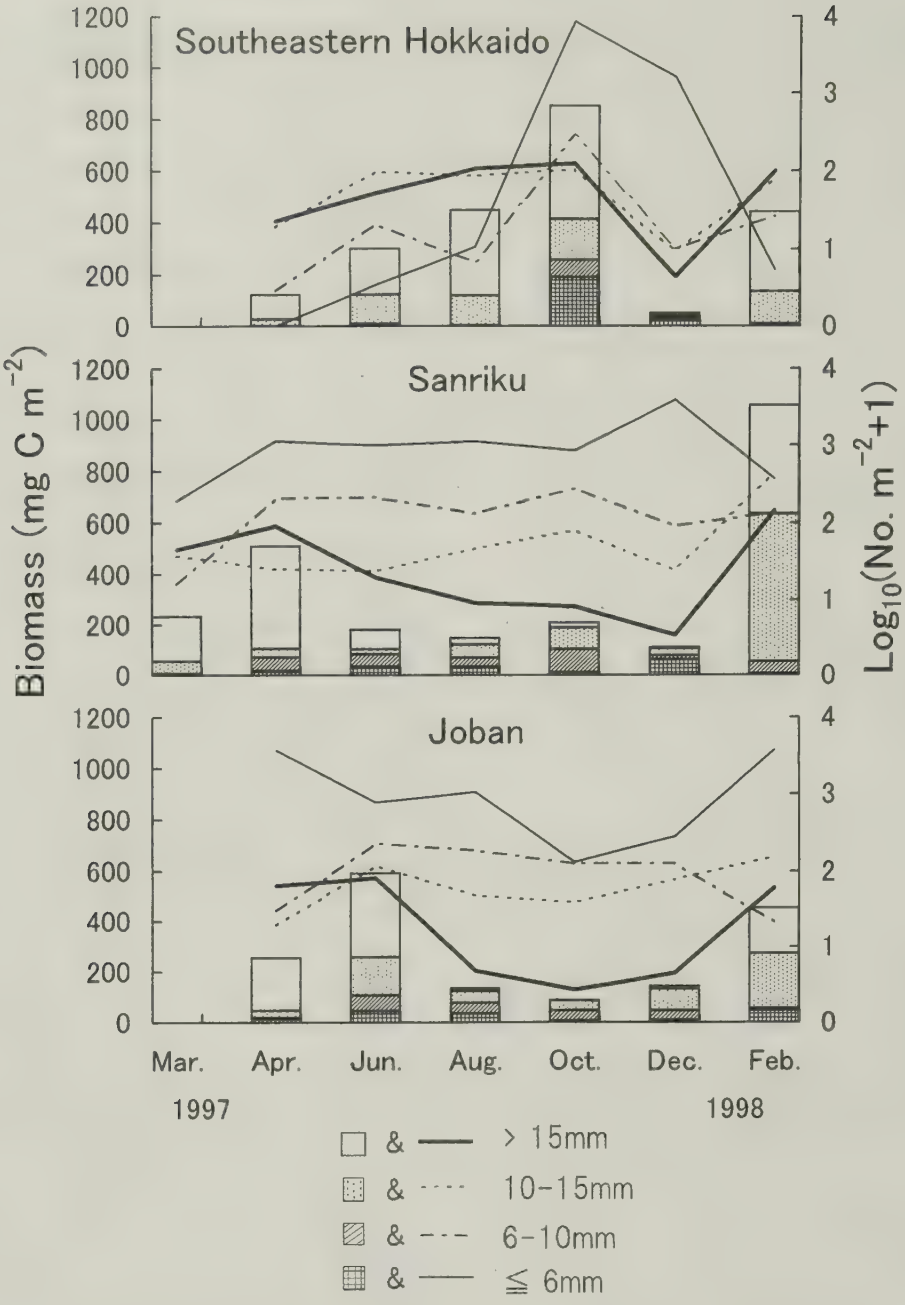

Fig. 5-2. Seasonal changes in the monthly average biomass (bars) and abundance (lines) by size class of *Euphausia pacifica* along the three coastal areas off northeastern Japan.

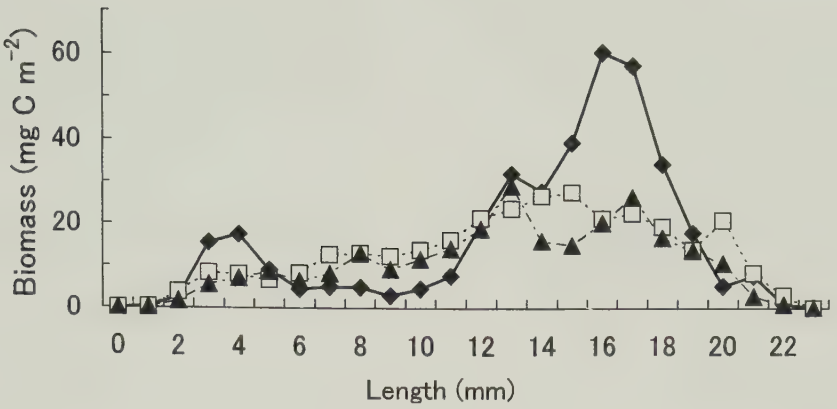

Fig. 5-3. Mean biomass for each size class of *Euphausia pacifica* along the three coastal areas off northeastern Japan. ◆: southeastern Hokkaido, □: Sanriku, ▲: Joban.

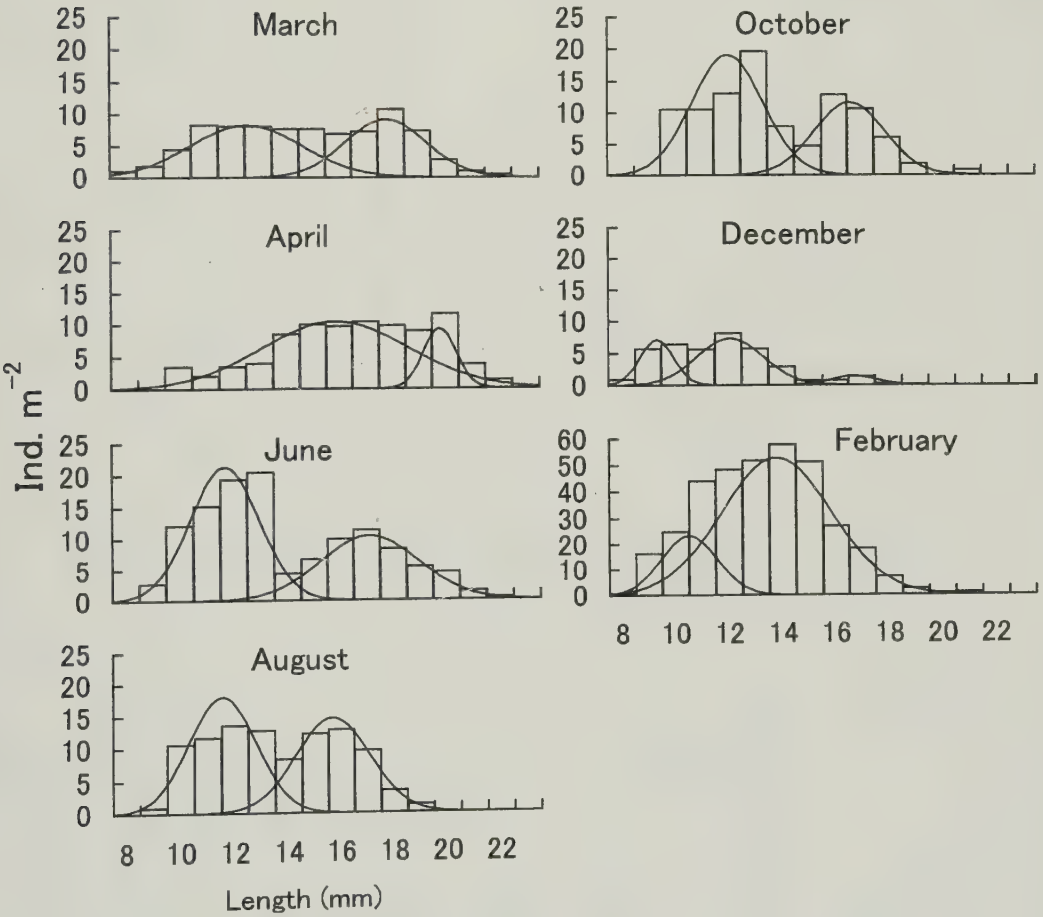

Fig. 5-4. Size-frequency distribution of adult *Euphausia pacifica* in the entire survey area off northeastern Japan. Hypothetical distribution curve of each cohort is superimposed using a computer program devised by Macdonald and Green (1988).

$$PM = \sum_{i=1} ((PM_i + PM_{i+1}) \times d_{i,\,i+1}/2) \quad (5.7)$$

where PM_i is daily each production and metabolism of ith survey, $d_{i,\,i+1}$ is days between ith survey and $(i+1)$th survey.

Results

Biomass

Off southeastern Hokkaido, the monthly biomass of *E. pacifica* increased from April to October, peaked at 852mg C m^{-2} in October and decreased after that (Fig. 5-2). Off Sanriku, the biomass was high in April (509mg C m^{-2}) and February (1,055 mg C m^{-2}), but was low from June through December (112-209 mg C m^{-2}). Off Joban, the biomass was high in April (254mg C m^{-2}), June (591mg C m^{-2}), and February (453mg C m^{-2}), but was low from August through December (90-104mg C m^{-2}). The relative contribution of large adults (>15mm) to the total biomass tended to be high in each coastal area when the total biomass was high.

Large adults of *E. pacifica* were most abundant in October off southeastern Hokkaido, and abundant in February, April and June off Sanriku and Joban (Fig. 5-2). So, high biomass tended to be recognized when large adults were abundant in each coastal area.

Annual mean biomass was 381mg C m^{-2}, 314mg C m^{-2} and 258mg C m^{-2} off southeastern Hokkaido, Sanriku and Joban, respectively (Table 5-1).

Annual mean biomass peaked among 13-19mm size classes commonly in each coastal area, with a

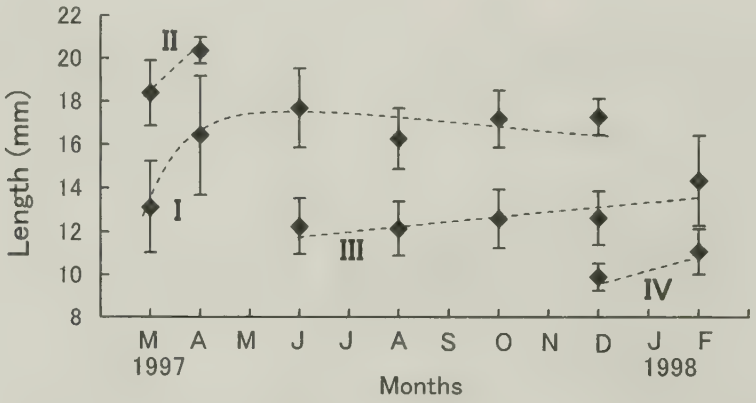

Fig. 5-5. Seasonal changes in the average length of each cohort of adult *Euphausia pacifica* estimated by size-frequency distributions in all coastal areas off northeastern Japan. Roman numerals indicate the cohort number. Lines: Hypothetical growth. Vertical bars: SD.

Table 5-1. Carbon budget (mg C m^{-2}) of *E. pacifica* along the three coastal areas off northeastern Japan during the survey period (313 or 356 days)

	SE Hokkaido (313 days)			Sanriku (356 days)			Joban (313 days)			Entire area (356 days)		
Mean biomass (B)	381			314			258			309		
		(% of P)	(% of A)		(% of P)	(% of A)		(% of P)	(% of A)		(% of P)	(% of A)
Somatic production (P_g)	1971	51.5%	25.7%	2178	56.3%	28.3%	1591	70.9%	30.0%	1983	57.7%	27.8%
Egg production (P_r)	1636	42.7%	21.3%	1414	36.5%	18.4%	410	18.3%	7.7%	1199	34.9%	16.8%
Moult production (P_e)	221	5.8%	2.9%	280	7.2%	3.6%	243	10.8%	4.6%	255	7.4%	3.6%
Gross production ($P=P_g+P_r+P_e$)	3829		49.9%	3872		50.3%	2243		42.3%	3438		48.2%
Routine Metabolism (M_{rtn})	2520		32.8%	2783		36.1%	2257		42.5%	2614		36.7%
Diurnal vertical migration metabolism (M_{dvm})	1325		17.3%	1044		13.6%	805		15.2%	1074		15.1%
Gross metabolism ($M=M_{rtn}+M_{dvm}$)	3846		50.1%	3827		49.7%	3062		57.7%	3688		51.8%
Assimillation ($A=P+M$)	7674			7699			5306			7126		
Ingestion ($I=A/0.84$)	9136			9166			6316			8483		
$P_g:B$	5.17			6.94			6.17			6.41		
$P:B$	10.05			12.34			8.70			11.12		
$P:M$	1.00			1.01			0.73			0.93		

second smaller peak among 3-5mm size classes off southeastern Hokkaido (Fig. 5-3). The relative biomass of size classes >10mm was considerably high, contributing 76.6-83.6% to the total in each coastal area.

Monthly mean biomass in all survey stations varied between 104 mg C m^{-2} (in December) to 685mg C m^{-2} (in February), and the annual mean biomass was 309mg C m^{-2} (Table 5-1).

Seasonal growth pattern

In the monthly average length-frequency distributions of adult *E. pacifica* in the all three coastal areas, two modal size groups were generally recognized (Fig. 5-4). It was difficult to rationally divide the size distribution for February into two modal groups based only on the length-frequency data. The groups for February were divided by considering the sequence of modal groups from June to December. Based on the modal growth pattern, average growth follows this pattern (Fig. 5-5): cohort I of

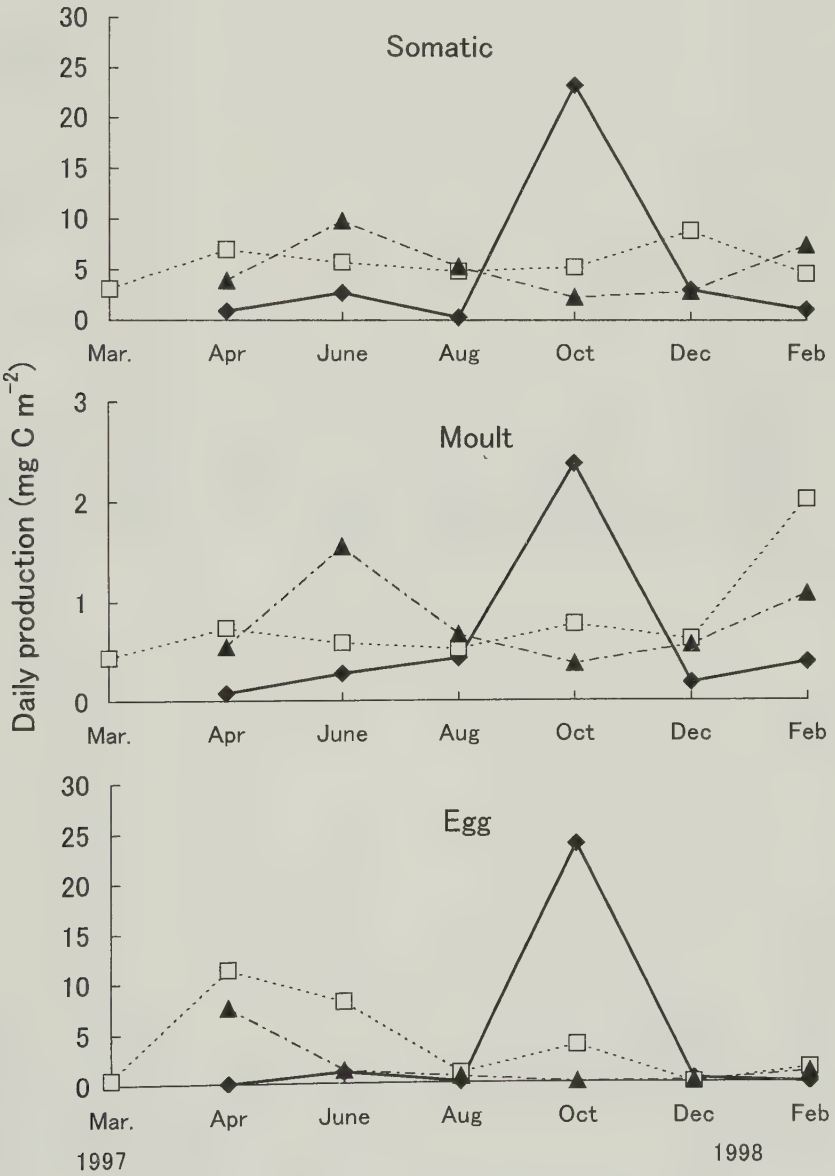

Fig. 5-6. Seasonal changes in daily production of somatic, moult and egg of *Euphausia pacifica* along the three coastal areas off northeastern Japan. The symbols are the same as shown in Fig. 5-3.

Table 5-2. Relative contribution (%) of each size class of *E.pacifica* to mean biomass (B), somatic producition (P_g), moult production (P_e), routine metabolism (M_{rtn}), diurnal vertical migration metabolism (M_{div}) and assimilation (A) achieved during survey period off SE Hokkaido

Development stage*	Size Class (mm)	%B	%P_g	%P_e	%M_{rtn}	%M_{div}	%A
Calyptopis	0～1	0.004	0.8	0.03	0.04	0	
	1～2	0.1	2.2	0.5	0.5	0	
	2～3	0.7	8.3	3.1	2.3	0.9	
Furcilia	3～4	4.1	30.3	17.3	12.4	6.0	
	4～5	4.6	24.5	16.1	11.2	6.4	
	5～6	2.4	9.8	5.8	4.2	3.5	
Immatures	6～7	1.2	4.0	2.1	1.6	2.7	
	7～8	1.3	3.9	2.2	1.8	2.5	
	8～9	1.3	3.3	2.0	1.6	2.0	≦10 mm
	9～10	0.8	1.7	0.9	0.8	1.2	40.6
Small adults	10～11	1.2	0.9	1.1	1.1	1.5	
	11～12	2.0	1.7	1.5	1.7	2.5	
	12～13	5.3	2.5	4.3	4.6	6.5	
	13～14	8.5	2.3	7.5	7.7	9.6	
	14～15	7.4	0.8	5.0	5.8	6.5	
Large adults	15～16	10.5	0.7	5.6	7.6	8.5	
	16～17	16.1	0.7	8.9	11.8	14.0	
	17～18	15.2	0.5	8.2	11.2	12.9	
	18～19	9.1	0.4	4.7	6.6	7.0	
	19～20	4.8	0.4	2.0	3.1	3.3	
	20～21	1.4	0.2	0.4	0.8	0.9	
	21～22	2.0	0.1	0.7	1.3	1.3	
	22～23	0.2	0.03	0.1	0.1	0.2	> 10 mm
	23～24	0.04	0	0.01	0.02	0.02	59.4
	Total	100	100	100	100	100	100

*Developmental stages should be considered as a rough guide.

Table 5-3. Relative contribution (%) of each size class of *E.pacifica* to mean biomass (B), somatic producition (P_g), moult production (P_e), routine metabolism (M_{rtn}), diurnal vertical migration metabolism (M_{div}) and assimilation (A) achieved during survey period off Sanriku

Development stage*	Size Class (mm)	%B	%P_g	%P_e	%M_{rtn}	%M_{div}	% A
Calyptopis	0～1	0.002	0.4	0.01	0.02	0	
	1～2	0.1	1.5	0.3	0.3	0	
	2～3	1.2	12.2	3.8	3.4	3.2	
Furcilia	3～4	2.7	16.8	7.7	6.3	6.8	
	4～5	2.6	11.6	6.5	5.2	4.9	
	5～6	2.1	7.4	5.2	4.1	3.4	
Immatures	6～7	2.6	7.7	4.6	3.8	6.0	
	7～8	4.0	10.0	6.7	5.5	6.6	
	8～9	4.2	9.0	5.9	5.0	6.3	≦10 mm
	9～10	3.9	7.5	5.4	4.7	5.1	44.6
Small adults	10～11	4.4	1.8	5.0	4.6	5.5	
	11～12	5.2	1.4	5.3	5.1	5.5	
	12～13	6.8	1.3	6.4	6.3	6.6	
	13～14	7.6	1.2	6.4	6.7	6.6	
	14～15	8.6	1.4	6.5	7.1	6.5	
Large adults	15～16	8.9	1.5	6.1	7.0	6.0	
	16～17	6.9	1.1	4.4	5.3	4.7	
	17～18	7.2	1.4	4.2	5.4	4.6	
	18～19	6.2	1.8	3.3	4.4	3.7	
	19～20	4.4	1.5	2.1	3.0	2.4	
	20～21	6.7	1.1	2.7	4.3	3.7	
	21～22	2.7	0.4	1.2	1.8	1.5	
	22～23	1.0	0.1	0.4	0.6	0.5	> 10 mm
	23～24	0.002	0	0.001	0.001	0.001	55.4
	Total	100	100	100	100	100	100

*Developmental stages should be considered as a rough guide.

Table 5-4. Relative contribution (%) of each size class of *E.pacifica* to mean biomass (B), somatic producition (P_g), moult production (P_e), routine metabolism (M_{rtn}), diurnal vertical migration metabolism (M_{div}) and assimilation (A) achieved during survey period off Joban

Development stage*	Size Class (mm)	%B	%P_g	%P_e	%M_{rtn}	%M_{div}	% A
Calyptopis	0～1	0.007	1.0	0.02	0.03	0	
	1～2	0.1	1.4	0.2	0.3	0	
	2～3	0.7	6.8	1.7	1.7	1.4	
Furcilia	3～4	2.2	13.4	4.3	4.0	4.9	
	4～5	2.8	12.3	6.3	5.3	4.8	
	5～6	3.4	11.7	7.1	5.8	5.3	
Immatures	6～7	2.5	7.2	4.3	3.6	5.1	
	7～8	3.2	7.9	5.1	4.3	5.6	
	8～9	5.0	10.8	7.5	6.4	7.6	≦10 mm
	9～10	3.6	6.8	4.8	4.2	5.4	46.9
Small adults	10～11	4.5	2.8	5.7	5.1	6.0	
	11～12	5.5	2.3	6.3	5.8	6.4	
	12～13	7.3	2.9	7.4	7.2	7.6	
	13～14	11.4	5.4	10.1	10.3	10.6	
	14～15	6.2	0.9	4.8	5.2	4.9	
Large adults	15～16	5.8	1.0	3.9	4.5	3.7	
	16～17	7.9	1.6	5.0	6.0	4.8	
	17～18	10.3	1.8	6.1	7.7	6.0	
	18～19	6.6	0.9	3.8	4.9	3.8	
	19～20	5.4	0.7	2.8	3.8	3.2	
	20～21	4.2	0.4	2.1	3.0	2.2	
	21～22	1.1	0.1	0.5	0.8	0.7	
	22～23	0.4	0.03	0.2	0.3	0.2	> 10 mm
	23～24	0	0	0	0	0	53.1
	Total	100	100	100	100	100	100

*Developmental stages should be considered as a rough guide.

about 13mm in March shows rapid growth through about 16mm in April to about 18mm in June with the growth rate being 0.077mm day^{-1} from March to April and 0.019mm day^{-1} from April to June. This cohort then shows no growth after June to December, and is likely to connect to cohort II of about 18mm in March if the seasonal growth pattern could be supposed to be invariable between years. Cohort II showed rapid growth (0.046mm day^{-1}) to about 20mm in April. There are two new cohorts in June (cohort III) and December (cohort IV) which seem to be spring-hatched and fall-hatched, respectively (see **Chapter 3**). Cohort III of about 12mm in June shows slow growth (0.008mm day^{-1}) to about 14mm in February. Cohort IV of about 10mm in December also shows slow growth (0.016mm day^{-1}) to about 11mm in February. Both of these newly-appearing cohorts are likely to connect to the cohort I of about 13mm in March if the seasonal growth pattern could be supposed to be invariable between years.

Production

Off southeastern Hokkaido, the production due to growth (P_g) was remarkably high (23.5mg C m^{-2}) in October, but was almost less than 3mg C m^{-2} in other months (Fig. 5-6). Higher P_g was observed in April (7.0mg C m^{-2}) and December (9.0mg C m^{-2}) off Sanriku and in June (9.9mg C m^{-2}) and February (7.6mg C m^{-2}) off Joban. The seasonal change off Sanriku and Joban was less dramatic than off south-

eastern Hokkaido. High P_g tended to be observed when high abundance of larvae occurred in each coastal area, and vice versa (see **Chapter 3**).

Off southeastern Hokkaido, the production due to moults (P_e) was high (2.4mg C m^{-2}) in October, but was almost less than 0.5mg C m^{-2} in other months (Fig. 5-6). Higher P_e was observed in February (2.0mg C m^{-2}) off Sanriku and, in June (1.6mg C m^{-2}) and next February (1.1mg C m^{-2}) off Joban. The seasonal change of P_e synchronized well with that of the biomass (Fig. 5-2) in each coastal area.

Off southeastern Hokkaido, the production due to eggs (P_r) was remarkably high (24.0mg C m^{-2}) in October, but was remarkably low in other months (Fig. 5-6). Off Sanriku, P_r was 11.3mg C m^{-2} in April and 8.1mg C m^{-2} in June, but was remarkably low in other months. Off Joban, P_r was 7.6mg C m^{-2} in April but remarkably low in other months. The seasonal change of P_r depended strongly on that of abundance of eggs in each coastal area (see **Chapter 3**).

The total production ($P = P_g + P_e + P_r$) during the survey period off southeastern Hokkaido (3,829mg C m^{-2}) was comparable with that off Sanriku (3,872mg C m^{-2}), but rather higher than that off Joban (2,243mg C m^{-2}) (Table 5-1). The rank of $P : B$ ratio during the survey period was Sanriku (12.34) > southeastern Hokkaido (10.05) > Joban (8.70). The production due to growth during the survey period ranged from 2,178mg C m^{-2} off Sanriku to 1,591mg C m^{-2} off Joban, contributing the highest proportion (51.5-70.9%) to the total production in each coastal area. The production due to moults during the survey period ranged from 280mg C m^{-2} off Sanriku to 221mg C m^{-2} off southeastern Hokkaido, contributing the lowest proportion (5.8-10.8%) to

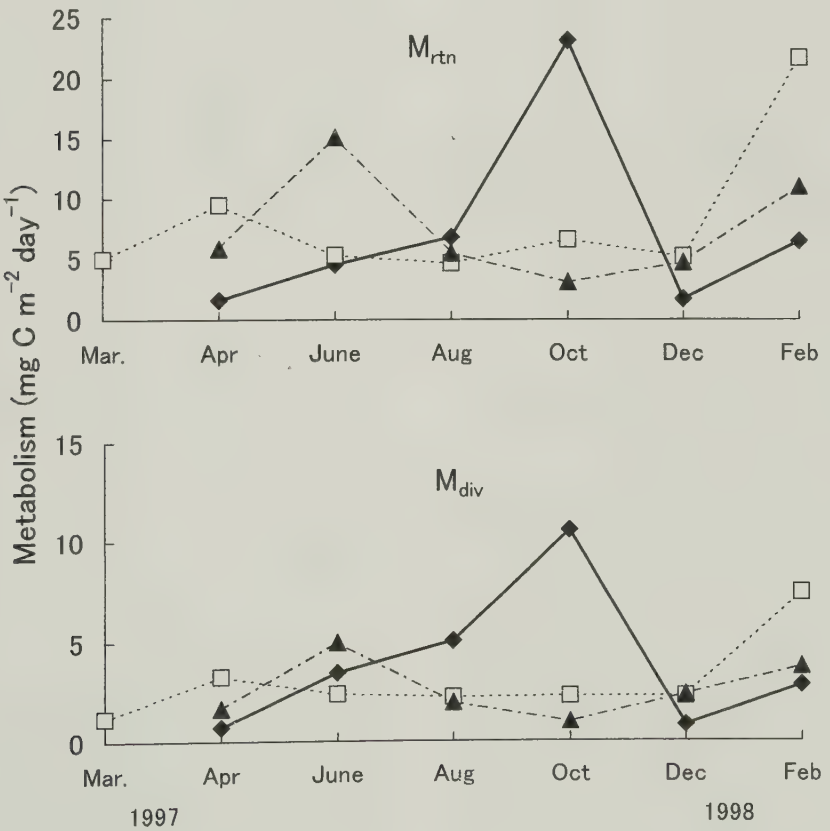

Fig. 5-7. Seasonal changes in carbon loss due to routine metabolism (M_{rtn}) and diurnal vertical migration metabolism (M_{div}) of *E. pacifica* along the three coastal areas off northeastern Japan. The symbols are the same as shown in Fig. 5-3.

Table 5-5. Relative contribution (%) of each size class of *E.pacifica* to mean biomass (B), somatic producition (P_g), moult production (P_e), routine metabolism (M_{rtn}), diurnal vertical migration metabolism (M_{div}) and assimilation (A) achieved during survey period off entire surveyarea

Development stage*	Size Class (mm)	%B	%P_g	%P_e	%M_{rtn}	%M_{div}	% A
Calyptopis	0～1	0.004	0.6	0.02	0.01	0	
	1～2	0.1	1.6	0.3	0.2	0	
	2～3	0.9	9.5	2.9	2.3	1.9	
Furcilia	3～4	2.8	19.0	8.8	7.1	5.8	
	4～5	3.1	15.0	8.6	6.6	5.3	
	5～6	2.4	8.9	5.8	4.4	3.7	
Immatures	6～7	2.0	6.4	3.8	3.0	4.5	
	7～8	2.8	7.6	5.0	4.0	4.8	
	8～9	3.3	7.8	5.3	4.4	5.0	≦10 mm
	9～10	2.5	5.2	3.8	3.1	3.5	42.4
Small adults	10～11	3.2	1.8	4.0	3.6	4.0	
	11～12	4.0	1.8	4.6	4.2	4.5	
	12～13	6.1	2.2	6.0	5.8	6.6	
	13～14	8.2	2.7	7.5	7.6	8.3	
	14～15	7.5	1.4	5.6	6.2	6.2	
Large adults	15～16	8.8	1.4	5.5	6.7	6.6	
	16～17	10.0	1.3	5.8	7.4	8.1	
	17～18	10.6	1.5	6.0	7.9	8.0	
	18～19	7.9	1.6	4.3	5.8	5.3	
	19～20	5.5	1.4	2.7	3.9	3.4	
	20～21	5.2	0.8	2.4	3.6	2.8	
	21～22	2.4	0.3	1.1	1.7	1.4	
	22～23	0.7	0.1	0.3	0.5	0.4	> 10 mm
	23～24	0.02	0	0.004	0.01	0.01	57.6
	Total	100	100	100	100	100	100

*Developmental stages should be considered as a rough guide.

the total production in each coastal area. The production due to eggs (1,636mg C m^{-2}) during the survey period off southeastern Hokkaido was slightly higher than that off Sanriku (1,414mg C m^{-2}), but about 4 times higher than that off Joban (410mg C m^{-2}). The total production across the entire survey area was 3,438mg C m^{-2} and the $P : B$ ratio was 11.12.

The relative contribution of each size class to the total somatic production during the survey period was high among 3-5mm size classes (25.8-54.8%) commonly in each coastal area (Tables 5-2-4). However, the relative contribution of size classes > 10mm was only 11.1-20.7% in each coastal area. The relative contribution of each size class to the total exuvial production during the survey period was high among 3-5mm size classes (33.4%) and 13-19mm (39.9%) off southeastern Hokkaido (Table 5-2). On the other hand, it was nearly constant across the wide size range (3-18mm) off Sanriku and Joban (Tables 5-3 and 4).

Metabolism

Off southeastern Hokkaido, the routine metabolism (M_{rtn}) was highest (23.3mg C m^{-2}) in October, but was less than 2mg C m^{-2} in April and December (Fig. 5-7). Higher M_{rtn} was observed in February (21.9mg C m^{-2}) off Sanriku and in June (15.2mg C m^{-2}) and February (11.1mg C m^{-2}) off Joban. The seasonal change of M_{rtn} synchronized well with that of the biomass (Fig. 5-2) in each coastal area.

Off southeastern Hokkaido, the diurnal vertical migration metabolism (M_{div}) was highest (10.6mg C m^{-2}) in October, but was less than 1mg C m^{-2} in

April and December (Fig. 5-7). Higher M_{div} was observed in February (7.5mg C m^{-2}) off Sanriku and in June (5.0mg C m^{-2}) off Joban. The seasonal change of M_{div} synchronized well with that of the biomass (Fig. 5-2) and M_{rtn} in each coastal area. The total metabolism ($M = M_{rtn} + M_{div}$) during the survey period off southeastern Hokkaido (3,846mg C m^{-2}) was comparable with that off Sanriku (3,827mg C m^{-2}), but higher than that off Joban (3,062mg C m^{-2}) (Table 5-2). The routine metabolism during the survey period ranged from 2,783mg C m^{-2} off Sanriku to 2,257mg C m^{-2} off Joban, contributing the highest proportion (32.8-42.5%) to the assimilation in each coastal area. The diurnal vertical migration metabolism during the survey period ranged from 1,325mg C m^{-2} off southeastern Hokkaido to 805mg C m^{-2} off Joban, contributing 13.6-17.3% to the assimilation in each coastal area. The total metabolism across the entire survey area was 3,688mg C m^{-2}, contributing 51.8% to the assimilation.

The relative contribution of each size class to the total routine metabolism during the survey period was high among 3-5mm size classes (23.6%) and 16-18mm (23.1%) off southeastern Hokkaido, but it was nearly constant across the wide size range (3-18mm) off Sanriku and Joban (Tables 5-2-4). The relative contribution of each size class to the total diurnal vertical migration metabolism during the survey period was similar to that to the total routine metabolism in each coastal area, but the relative contribution among 16-18mm (27%) was about 2 times higher than that among 3-5mm (12.4%) off southeastern Hokkaido.

Assimilation and ingestion

The assimilation (A) during the survey period off southeastern Hokkaido (7,674mg C m^{-2}) was comparable with that off Sanriku (7,699mg C m^{-2}), but rather higher than that off Joban (5,306mg C m^{-2}) (Table 5-1). The assimilation across the entire survey area was 7,126mg C m^{-2}. The ingestion (I) during the survey period ranged from 9,166mg C m^{-2} off Sanriku to 6,316mg C m^{-2} off Joban, and the ingestion across the entire survey area was 8,483mg C m^{-2}.

The relative contribution of larval size class ($\leqq$ 10mm) to the assimilation (thus also to the ingestion) during the survey period ranged from 41 to 47% in the coastal areas (Tables 5-2-5).

Discussion

Characteristics of biomass

High biomass was recognized when large adults were abundant in each coastal area (Fig. 5-2). The relative contribution of large adults to the total annual mean biomass was 51% across the entire survey area, while their relative contribution to the total annual mean abundance was only 2.6%. Therefore, the biomass is thought to be strongly affected by the occurrence of large adults which have a relatively high weight per individual. Annual mean biomass was low in the low latitudes due to the influence of the warmer Kuroshio waters through summer and fall which large adults avoid (see **Chapter 3**).

The biomasses of several euphausiid species from several regions are shown in Table 5-6. Water content and carbon content are assumed to be 80 % and 43 %, respectively and converted to carbon weight (mg) per square meter or dry weight (mg) per 1,000 cubic meters from original units in the literature (Brinton and Reid, 1986; Gomez-Gutierrez and Robinson, 1997; Heath, 1977; Tanasichuk, 1998a; Gomez-Gutierrez *et al.*, 1996; Hirota *et al.*, 1982; Lavaniegos, 1995; Mauchline, 1977; Siegel, 2000; Tanasichuk, 1998b). The annual mean biomass of *E. pacifica* in the coastal waters off northeastern Japan was lower than that at Saanich Island (Heath, 1977) and off Oregon (Mauchline, 1977) in the upstream California Current, but higher than that off southern California (Brinton, 1976) and off Baja California (Gomez-Gutierrez and Robinson, 1997) in downstream California Current. The tendency for the biomass of *E. pacifica* to be higher in the higher latitudes of the eastern Pacific is identical with the trend along the coastal waters off northeastern Japan.

The annual mean biomass of 1,090mg C m^{-2} for *E. pacifica* in Toyama Bay was about three times higher than that found along the coastal waters off northeastern Japan (Iguchi *et al.*, 1993). The annual mean abundance of eggs of *E. pacifica* was 2,749 inds m^{-2} in Toyama Bay (calculated from Table 1 in Iguchi *et al.* (1993)), which is nearly identical with

Table 5-6. Biomass and *P:B* ratios of euphausiids from net sampling surveys [*1]

Species	Geographic region	Biomass (mg C m^{-2})	*P:B* from growth	*P:B* from moults	*P:B* from eggs	References
Euphausia pacifica	Saanich Island, Canada	2025.3[*2]	2.6[*3]			Heath (1977)
Euphausia pacifica	Barkley Sound, Canada	301–624 (384)[*4]	6.4–16.7(11.0)	0.9–1.4 (1.2)[*5, 6]		Tanasichuk (1998a)
Euphausia pacifica	Oregon, USA	1125[*7]	8.7			Mauchline (1977)
Euphausia pacifica	Southern California, USA (Jan.)	17–163 (112)[*8]				Brinton and Reid (1986)
Euphausia pacifica	Southern California, USA (Apr.)	77–166 (107)[*8]				Brinton and Reid (1986)
Euphausia pacifica	Baja California, Mexico	38[*4]				Gomez-Gutierrez& Robinson (1997)
Euphausia pacifica	Toyama Bay, Japan	1,090	3.8	1.1	1.1	Iguchi and Ikeda (1999)
Euphausia pacifica	Northeastern Japan	258–381(309) [3,362–5,852 (4,300)][*9]	5.2–6.9 (6.4)	0.6–0.9 (0.8)	1.6–4.5 (3.9)	This study
Euphausia similis	Sagami Bay, Japan	102	4.8			Hirota *et al.* (1990)
Euphausia nana	Sagami Bay, Japan	25[*8]				Hirota *et al.* (1982)
Euphausia lucens	Benguela Current	[9,750–47,290 (22,480)][*9]	3.9–8.9 (6.9)	3.2–3.3 (3.3)[*5]	0.3–1.0 (0.6)[*10]	Stuart and Pillar (1988)
Euphausia superba	Antarctic Peninsula	387–527 (457)	0.83–1.1 (1.0)			Siegel (1992)
Euphausia superba	Elephant Island	86–2,683(903)[*8]				Siegel (2000)
Euphausia superba	Antarctic, Indian Ocean		1.53			Miller *et al.* (1985)
Meganyctiphanes norvegica	North Atlantic and North Sea	[140–13,990 (1,983)][*9]	1.3–6.3 (3.5)			Lindley (1982)
Meganyctiphanes norvegica	Rockall Trough, Britain		1.6			Mauchline (1985)
Nematoscelis microps	Sagami Bay, Japan	30[*8]				Hirota *et al.* (1982)
Nematoscelis gracilis	Sagami Bay, Japan	11[*8]				Hirota *et al.* (1982)
Nematoscelis megalops	Rockall Trough, Britain		3.4			Mauchline (1985)
Nematobrachion boopis	Rockall Trough, Britain		1.2			Mauchline (1985)
Nyctiphanes simplex	Baja California, Mexico	44[*4]	12.7	2.1[*5]	0.3[*10]	Lavaniegos (1995)
Nyctiphanes simplex	Baja California, Mexico	17[*4]	6.99			Gomez-Gutierrez *et al.* (1996)
Nyctiphanes australis	Storm Bay, Tasmania	[5,389][*9]	14.5	4.2[*5]	0.9[*10]	Hosie and Ritz (1983)
Nyctiphanes couchi	North Sea	[150–2,070 (700)][*9]	4.0–5.5 (4.5)			Lindley (1982)
Stylocheiron maximum	Rockall Trough, Britain		2.5			Mauchline (1985)
Thysanopoda acutifrons	Rockall Trough, Britain		2.3			Mauchline (1985)
Thysanoessa spinifera	British Columbia	147–547 (323)[*4]	11.1–35.0 (18.7)	0.8–1.8 (1.0)[*5, 6]		Tanasichuk (1998b)
Thysanoessa inermis	North Sea & east coast of USA	[690–2,370 (1,112)][*9]	1.4–6.1 (2.8)			Lindley (1980)
Thysanoessa longicaudata	North Atlantic	[70–2,360 (1,088)][*9]	1.2–11.6 (4.1)			Lindley (1978)
Thysanoessa longicaudata	Rockall Trough, Britain		6.4			Mauchline (1985)
Thysanoessa raschi	Gulf of St. Lawrence	[470][*9]	3.8			Berkes (1977)
Thysanoessa raschi	North Sea & east coast of USA	[310–1,600 (778)][*9]	1.3–10.4 (4.0)			Lindley (1980)

[*1] Note that mean values are shown in parentheses, and some values are converted from original ones to compare with the standardized units or assumptions described in the literature or below this table.

[*2] Conversion from mg WW m^{-3}

[*3] Recalculated value by Iguchi and Ikeda (1999)

[*4] Conversion from mg DW m^{-2}

[*5] Assuming that moult carbon content to be 23 % of DW.

[*6] Assuming that proportion of body DW lost per molting to be 4% becaue of the possibility of overestimating of the proportion (10.6–11.6 %) in the literature (see Iguchi and Ikeda (1999)) .

[*7] Conversion from mg DW 1000m^{-3}

[*8] Conversion from mg WW m^{-2}

[ ][*9] mg DW 1000m^{-3}

[*10] Assuming that proportion of egg carbon content to be 47 % of DW.

the value of 2,894 inds m^{-2} for the entire survey area off northeastern Japan. However the annual mean abundance of adults in Toyama Bay (822 inds m^{-2}) is about seven times higher than that of the entire survey area off northeastern Japan (122 inds m^{-2}), so such large difference in annual mean biomass is thought to attribute to the large difference in annual mean abundance of adults. The mortality rate of fall-winter hatching may be higher than that of spring hatching off northeastern Japan because of unfavorable feeding condition during fall and winter as shown by the low abundance of phytoplankton, microzooplankton and mesozooplankton (Kasai *et al.*, 2001; Kotani *et al.*, 1996; Odate, 1994). Therefore, the annual average recruitment rate off northeastern Japan is suggested to be lower than that in Toyama Bay where spawning occurred limitedly in spring phytoplankton bloom (Iguchi *et al.*, 1993).

Off the Pacific coast of Japan, the biomass of *E. pacifica* is much higher than that of southern warmer species in Sagami Bay (Hirota *et al.*, 1982; Hirota *et al.*, 1990) (Table 5-6). However, no latitudinal trend is found between different species in the global level. For example, the biomass of subarctic species such as *Thysanoessa rachi* and *T. inermis* in the north Atlantic (45-60°N) is much lower than the mean biomass of subarctic-transitional *E. pacifica* off northeastern Japan (36-43°N). It should noted, however, that subarctic species in the north Atlantic studied by Lindley (1978; 1980; 1982) were only sampled the upper 10m layer by day and night, which may have led to underestimation of euphausiid biomass due to the vertical migratory behavior. The survey using with the same gear and methods is needed to compare the biomass of euphausiid species correctly.

Characteristics of production and assimilation

The relative contribution of larval and immature specimens ($<$10mm) of *E. pacifica* to the total somatic production during the survey period was high (79-89%), although their contribution to the total annual mean biomass was only 14-24% in each coastal area. This is due to the high growth rate of larvae and immature specimens as compared to adult specimens. This tendency was also recognized for *E. pacifica* from Barkley Sound, where the annual production due to growth and moults of larval and immature specimens ($<$9mm) showed the high proportion to the total (25-72% and 7-46%), although their annual mean biomass showed the low proportion to the total (14-24%) from 1991 to 1997 (Tanasichuk, 1998a).

Annual $P_g : B$, $P_e : B$ and $P_r : B$ ratios of several euphausiids are shown in Table 5-6. The previous measurements were standardized to carbon units by assuming the same carbon content as *E. pacifica* in this study: 43% of DW for the body, 23% of DW for moults, and 47% of DW of eggs.

The annual $P_g : B$ ratio tends to be high (ca. 9-15) for euphausiids that show continuous occurrences of larvae throughout the year and high growth rates, such as *E. pacifica* and *Thysanoessa spinifera* off Barkley Sound (Tanasichuk, 1998a; 1998b), *E. pacifica* off Oregon (Mauchline, 1977), *N. simplex* off Baja California (Gomez-Gutierrez and Robinson, 1997; Lavaniegos, 1995) and *Nyctiphanes australis* off Storm Bay, Tasmania (Hosie and Ritz, 1983). Meanwhile, the annual $P_g : B$ ratio tends to be low (ca. 1-4) for euphausiids which have short spawning periods and slow or long stagnated growth, such as *E. superba* (Miller *et al.*, 1985; Siegel, 1992), *M. norvegica* (Lindley, 1982; Mauchline, 1985) and *Thysanoessa spp.* (except for *T. longicaudata* in the North Atlantic Ocean) (Lindley, 1978; 1980). The $P_g : B$ ratio (5.2-6.9) of *E. pacifica* along the coastal waters off northeastern Japan was intermediate between these two groups due to the stagnant growth of adults during summer-winter coupled with the continuous occurrence of larvae which show high growth rate throughout the year off Sanriku and Joban and the considerably numerous larvae occurring in October off southeastern Hokkaido (see **Chapter 3**). In Toyama Bay seasonal growth pattern of adult *E. pacifica* is similar to that off northeastern Japan but the occurrence of larval stages was limited only in spring (Iguchi *et al.*, 1993). So, $P_g : B$ ratio in Toyama Bay (3.8) is rather lower than that off northeastern Japan (Table 5-6).

The annual $P_e : B$ (ca. 1.0) of *E. pacifia* both in the eastern and western Pacific Ocean was much lower than that of *N. australis* (4.2) in Storm Bay and *E. lucens* (3.2-3.3) in the Benguela Current. This was mainly due to the long interval of moults

in *E. pacifica* as compared with that in *N. australis* and *E. lucens*. The interval in *E. pacifica* was 3-10 days for larvae-immatures and 8-22 days for adults along the coastal waters off northeastern Japan, and was 3-4 days for larvae-immatures and 4-6 days for adults in *N. australis* and *E. lucens*.

Iguchi and Ikeda (1999) showed that the relative proportion of egg production to the total production ($P_g + P_c + P_r$) in *E. pacifica* was 20.6% in Toyama Bay, which is comparable to the value of 26.5% for the same species in the northern North Pacific (Lasker, 1966) and thus supposed that *E. pacifica* is a euphausiid characterized by a higher investment of carbon in egg production. *E. pacifica* along each coastal area off northeastern Japan also showed high proportion of egg production (18-43%) to the total production despite the limited spawning season. The low exuvial production due to relatively long interval of moults mentioned above is thought to increase the relative proportion of egg production in *E. pacifica*. The annual $P_r : B$ ratio (1.6-4.5) of *E. pacifica* along the coastal waters off northeastern Japan was higher than that (1.1) in Toyama Bay. This may attribute to unfavorable recruitment or underestimation of biomass due to cohesive aggregation along the coastal waters off northeastern Japan as compared with Toyama Bay mentioned above.

Metabolism of *E. pacifica* had been only calculated for Toyama Bay population by Iguchi and Ikeda (1999). $P : M$ ratio (0.73-1.0) along each coastal waters off northeastern Japan during survey period was significantly higher than that in Toyama Bay (0.41) (Table 5-1). One of the reasons attribute to higher $P_g : B$ and $P_r : B$ ratios off northeastern as mentioned above. The other reason is that both $M_{rtn} : B$ and $M_{div} : B$ ratios along the coastal waters off northeastern Japan (6.7-8.9 and 3.1-3.5, respectively) is lower than that in Toyama Bay (10.0 and 4.8, respectively). Lower $M_{rtn} : B$ and $M_{div} : B$ ratios off northeastern Japan attribute to lower habitat temperatures or lower coefficient a in equations (5. 5) (e. g. average of 6.7℃ off northeastern Japan vs. 8.0℃ in Toyama Bay for large adults) and shorter diurnal vertical migration or coefficient d in equation (5. 6) (e.g. average of 0.31km off northeastern Japan vs. 0.4-0.6km in Toyama Bay for large adults), respectively. However it should be noted that the shorter diurnal vertical migration is closely related to shallow sea bottom depths at onshore stations which could interrupt descending toward deeper depths in daytime usually conducted in offshore area.

Chapter 6. Feeding of *Euphausia pacifica*

Endo (1981) and Nakagawa *et al.* (2001) studied the seasonal changes in stomach contents of *Euphausia pacifica* in Sanriku waters. Off northeastern

Table 6-1. Locations of stations, times of sampling, number of samples and total length of *Euphausia pacifica* examined for the southeastern Hokkaido and Joban waters

	Latitude	Longitude	Depth (m)	Day	Time	Number of samples	Range of total length (mm)	Mean total length ±SD
SE Hokkaido	42°20'N	143°45'E	295	Apr. 15 '97	2:47	20	13.5–21.0	17.4±2.6
	42°30'N	145°00'E	1790	Jun. 21,'97	21:58	9	11.7–18.9	16.1±2.3
	42°40'N	144°55'E	540	Aug. 6,'97	21:29	20	13.3–19.5	16.4±1.6
	42°40'N	144°55'E	540	Oct. 1,'97	0:08	20	12.6–18.5	16.7±1.6
	42°40'N	144°55'E	540	Dec. 9,'97	18:21	10	12.0–18.4	14.6±2.0
	42°40'N	144°55'E	540	Feb. 25,'98	22:04	20	14.5–20.3	16.4±1.5
Joban	37°35'N	141°36'E	219	Apr. 22,'97	0:43	20	13.2–18.1	15.8±1.2
	36°50'N	141°15'E	179	Jun. 24,'97	0:09	20	12.5–22.3	16.8±2.2
	36°50'N	141°16'E	200	Aug. 2,'97	1:26	20	10.1–14.3	11.8±1.1
	36°50'N	141°17'E	208	Oct. 5,'97	20:43	20	12.0–17.0	13.4±1.3
	36°50'N	141°17'E	208	Dec. 11,'97	22:40	8	10.0–12.6	11.2±1.0
	36°50'N	141°16'E	200	Feb. 28,'98	22:35	20	14.0–17.2	15.7±1.0

Japan, however, the food habits of *E. pacifica* have been studied only in Sanriku waters. Studies on the comparison of the food habits of *E. pacifica* between different water masses is important to understand the structure of marine ecosystems off northeastern Japan.

In this chapter, seasonal changes in stomach contents of *E. pacifica* was surveyed in the coastal waters off southeastern Hokkaido and Joban. From the results, how diets and feeding behavior change according to ambient food conditions were examined. In addition, the significance of ingestion of copepods by *E. pacifica* was compared between the coastal waters off northeastern Japan.

Materials and Methods

Cylindrical-conical net samples collected bimonthly from April 1997 to February 1998 in the southeastern Hokkaido waters (about 42°40'N) and the Joban waters (about 36°50'N) (see **Chapter 3**) were used for the analysis of stomach contents of *Euphausia pacifica* (Table 6-1). The profiles of temperature and salinity were determined using CTD (Sea-Bird) or STD (Alec Electronics).

A 100 ml water sample was collected from each of 6 depths (0, 10, 20, 30, 50, 75m), filtered through a Whatman GF/F glass fiber filter, and analyzed by the method of Yentsch and Menzel (1963) with a Hitachi 139 spectrofluorometer for chlorophyll *a*. *Chlorophyll a* was integrated over the upper 75 m, and then averaged for each cruise.

Eight to ten adult *E. pacifica* were sorted randomly from each station, and their total length, from the anterior tip of the rostrum to the distal end of the telson, was measured. A total of 207 stomachs were dissected out and the contents spread on glass slides. Stomachs were examined under a dissecting microscope, and scored into 5 classes based on their fullness: empty stomachs (class 0), less than 25% full (class I), 25-50% full (class II), 50-75% full (class III), more than 75% full (class IV).

Food organisms were identified, enumerated and dimensions measured to allow calculation of both the total carbon content of the stomach contents and the relative contribution of the various prey types. The carbon contents of diatoms and dinoflagellates were estimated from cell volumes according to Strathmann (1967). Tintinnid carbon was estimated from the lorica volume according to Verity and Langdon (1984). Invertebrate eggs found in the stomachs were thought to be copepod eggs and carbon content was estimated from the egg size using a conversion factor of 0.14 pgC μm^{-3} (Kiorboe *et al.*, 1985). Copepods in the stomach were identified from their hard structures, mandibles, and their number was determined from the number of pairs of mandible blades of a given size. Total length of copepods was measured when found intact in the stomach. The carbon content of copepods was obtained by estimating the prosome length from the width of the mandible blades using the equation of Karlson and Bamstedt (1994), then calculating the dry mass from the prosome length of the copepod and assuming that 46% of the dry mass was carbon (Vidal, 1980). The carbon contents of intact copepods in the stomach were calculated from the total length using the equation of Hirota (1986).

Body carbon of *E. pacifica* was estimated from the total length using the equation of total length vs. dry weigh from Iguchi and Ikeda (1995) and conversion factor from the dry weight to carbon weight in different size classes of *E. pacifica* from Iguchi and Ikeda (1998).

Daily carbon ingestion of *E. pacifica* was calculated based on the gut passage time of 1.08 hr (Willason and Cox, 1987) and constant feeding limited from sunset to sunrise.

Results

Along the coastal waters off southeastern Hokkaido, waters with temperatures less than 2℃ occurred from the surface to 300m depth and coastal Oyashio waters with salinities less than 33.0 PSU occurred in the upper layer shallower than 100m in April (Fig. 6-1). Surface water temperatures rose from April to October. Surface water temperature was about 13℃ but less than 5℃ in the deeper layer than 75m in October. The surface water temperatures dropped after October and coastal Oyasshio waters with temperatures less than 1℃ and salinities less than 33.0 PSU in the upper layer than 50m. Along the coastal waters off Joban, water temperature in the total water column rose from April to Oc-

tober and the surface water temperature was about 22℃ in August and October. Waters with temperatures higher than 5℃ and salinities higher than 33.7 PSU were dominant from April to December. However, waters with temperatures less than 7℃ and salinities less than 33.7 PSU occurred in the upper layer than 30m.

Along the coastal waters off southeastern Hokkaido, chlorophyll *a* concentration was extremely high, 11.7 μ gl^{-1} in the surface layer in April and it was 4.2 μ gl^{-1} in 30m (Fig. 6-1). However, it was less than 0.5 μ gl^{-1} over the total water column in August. It was 1.4 μ gl^{-1} over the surface layer in October and 0.8 μ gl^{-1} in the upper layer than 50min December. It was less than 0.4 μ gl^{-1} in the total water column in February. Along the coastal waters off Joban, chlorophyll *a* concentration was 1.7 μ gl^{-1} in the surface layer in April and it was 0.7-0.9 μ gl^{-1} in 30-50m. However, it was less than 0.3 μ gl^{-1} in the total water column from August to December. It was 0.91-0.96 μ gl^{-1} in 30-50m. Thus, chlorophyll *a* concentration off the southeastern Hokkaido tended to be higher than that off Joban throughout the year.

Along the coastal waters off southeastern Hokkaido, the percentage of *E. pacifica* with a half or more stomach fullness (classes III and IV) was 100 % in February and it was 80 % in April and August (Fig. 6-2). On the other hand, the percentage of *E. pacifi-*

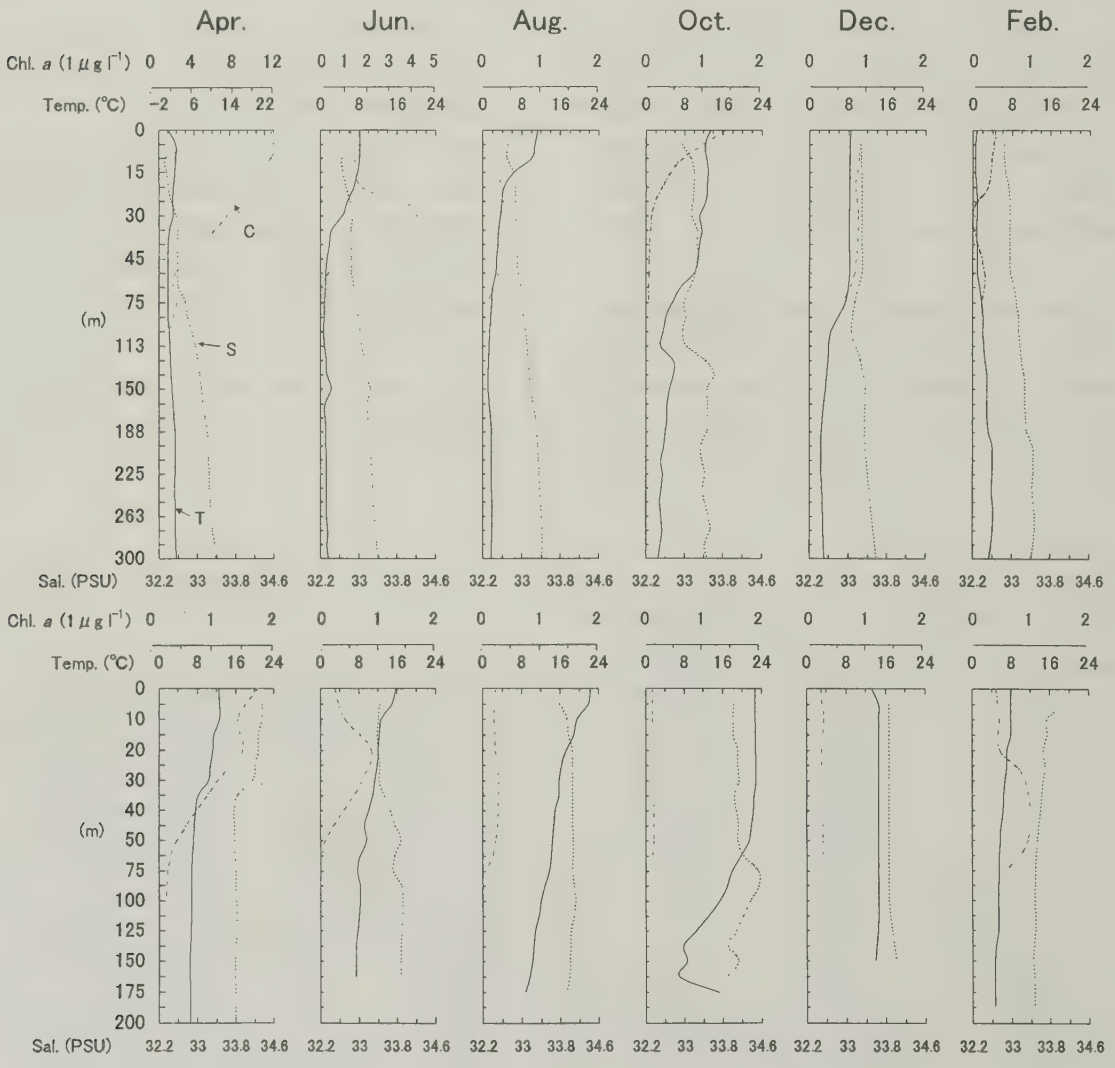

Fig. 6-1. Vertical profiles of water temperature, salinity and chlorophyll *a* in the southeastern Hokkaido waters (top) and Joban waters (bottom).

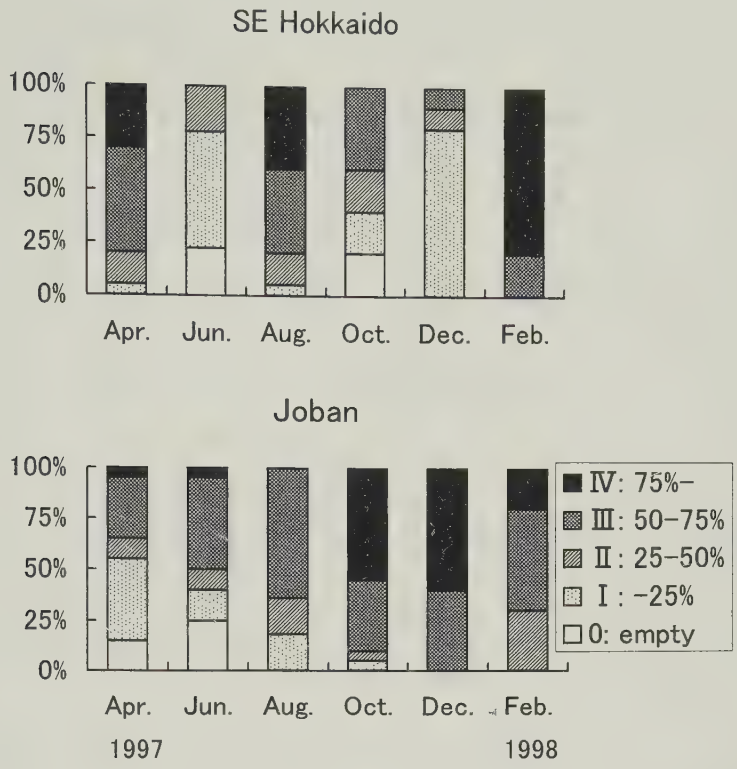

Fig. 6-2. Seasonal change in the stomach fullness composition of *Euphausia pacifica*.

ca with empty or a quarter stomach fullness (classes 0 and I) was 79 % and 80 % in June and December, respectively. Along the coastal waters off Joban, the percentage of *E. pacifica* with a half or more stomach fullness (classes III and IV) was 90 % and 100 % in October and December, respectively. On the other hand, the percentage of *E. pacifica* with empty or a quarter stomach fullness (classes 0 and I) was 65 % and 40 % in April and June, respectively.

Identifiable food items found in the stomach contents of *E. pacifica* were classified into 9 groups (diatoms, dinoflagellates, tintinnids, invertebrate eggs, copepod mandibles, foraminiferans, silicoflagellates, copepod nauplii and appendicularian houses). Frequency of occurrence of diatoms, dinoflagellates and tintinnids tended to be high throughout the year off both coastal waters and that of diatoms was generally higher than 70% off the southeastern Hokkaido (Table 6-2). The frequency occurrence of copepod mandibles off Joban was higher than that off southeastern Hokkaido throughout the year except February and August. Copepod nauplii occurred only in August off Joban and in October off southeastern Hokkaido.

Along the coastal waters off southeastern Hokkaido, diatoms in the stomach of *E. pacifica* were abundant (154 cells krill^{-1}) (Fig. 6-3). Dinoflagellates were abundant in August (24 cells krill^{-1}) and February (14 cells krill ^{1}). Tintinnids were abundant in October (19 cells krill ^{1}) and February (21 cells krill ^{1}). Invertebrate eggs were abundant in October (0.5 inds krill^{-1}) and February (0.4 inds krill^{-1}). Copepods were abundant in August and October (both 0.4 inds krill^{-1}) but were lower than those off Joban throughout the year.

Along the coastal waters off Joban, diatoms in the stomach of *E. pacifica* were abundant in February (121 cells krill^{-1}) and October (25 cells krill^{-1}) (Fig. 6-3). However they were scarce from April to August and in December. Dinoflagellates were abundant from April to August (3.4-8.5 cells krill^{-1}) but were scarce from October to February (0.9-1.6 cells

Table 6-2. Frequency of occurrence (%) of identifiable food items in gut contents of *Euphausia pacifica*

	Apr.'97	Jun.'97	Aug.'97	Oct.'97	Dec.'97	Feb.'98
Diatoms						
SE Hokkaido	100	67	90	75	80	80
Joban	80	5	15	90	100	100
Dinoflagellates						
SE Hokkaido	65	0	100	75	20	100
Joban	45	30	40	55	100	100
Foraminiferans						
SE Hokkaido	0	0	9	5	10	80
Joban	5	5	0	20	13	10
Tintinnids						
SE Hokkaido	45	44	100	75	70	100
Joban	10	45	30	10	50	70
Invertebrate eggs						
SE Hokkaido	15	0	40	20	20	45
Joban	0	15	35	20	30	25
Copepod mandibles						
SE Hokkaido	0	11	35	10	0	25
Joban	20	35	15	35	25	20
Copepod nauplii						
SE Hokkaido	0	0	0	5	0	0
Joban	0	0	35	0	0	0
Silicoflagellates						
SE Hokkaido	5	0	5	70	0	10
Joban	35	0	10	5	100	45
Appendicularian houses						
SE Hokkaido	0	0	10	10	0	0
Joban	35	5	0	70	88	0

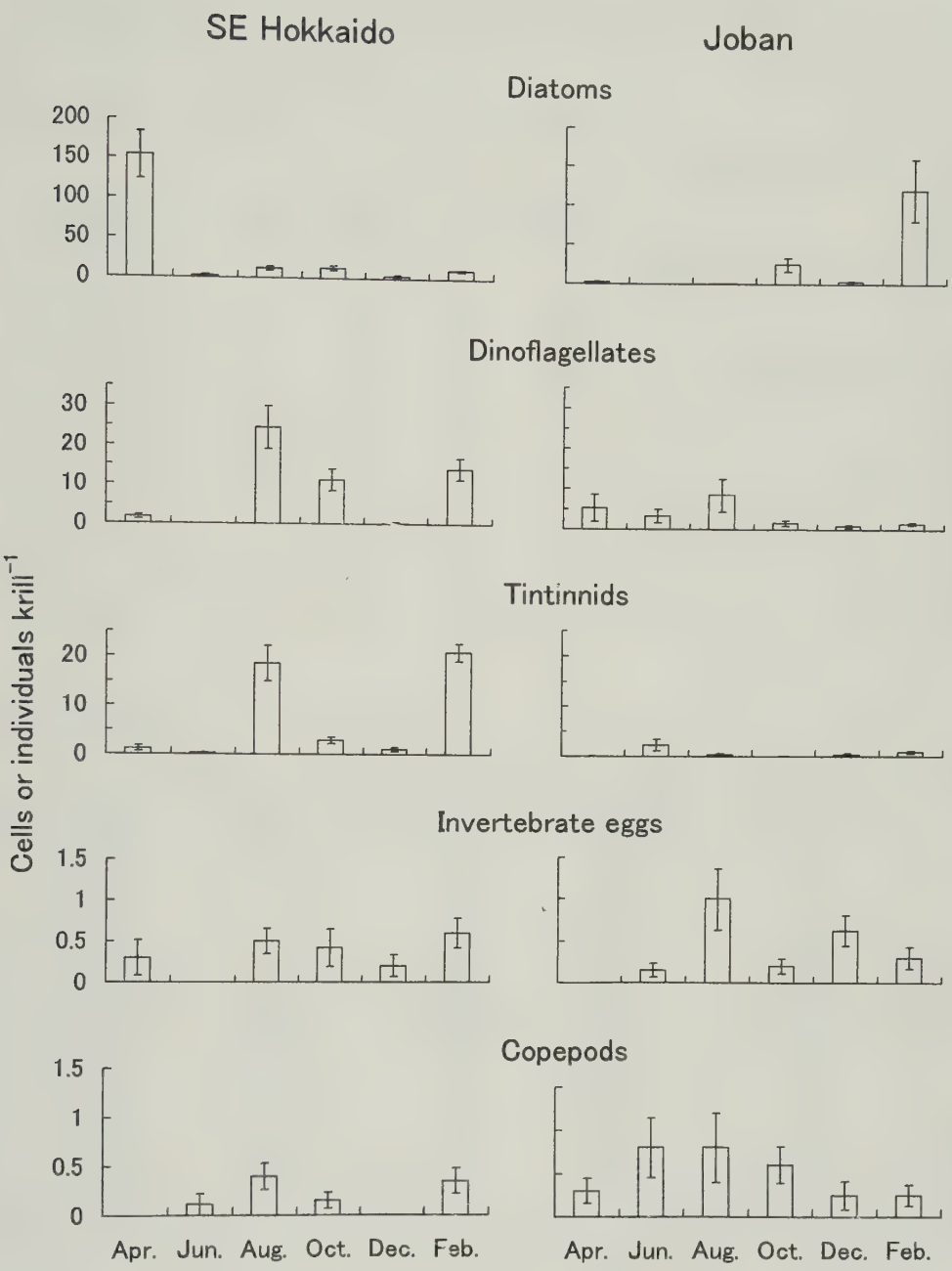

Fig. 6-3. Seasonal change in mean number of each identifiable food item in the gut contents of *Euphausia pacifica* individuals. Vertical bar represents ±1 SE.

Table 6-3. Mean total volumes of diatoms, dinoflagellates and tintinnids, mean diameter of invertebrate eggs, and mean prosome length of copepods in the stomach of *Euphausia pacifica* individuals.

	Apr.'97	Jun.'97	Aug.'97	Oct.'97	Dec.'97	Feb.'98
Diatom volume ($\times 10^3 \mu m^3$)						
SE Hokkaido	11.2(0.3)*	3.7(1.7)	2.4(0.3)	9.9(1.0)	6.3(2.0)	3.5(0.4)
Joban	6.8(1.3)	0.3(0)	5.2(3.4)	1.8(0.2)	6.3(1.7)	1.6(0.1)
Dinoflagellate volume ($\times 10^3 \mu m^3$)						
SE Hokkaido	37(7)		3(2)	10(3)	2(1)	18(3)
Joban	8(3)	51(34)	25(10)	32(13)	319(191)	219(72)
Tintinnid volume ($\times 10^3 \mu m^3$)						
SE Hokkaido	167(34)	190(32)	19(4)	208(48)	398(116)	131(6)
Joban	761	18(1)	36(9)	66	20(3)	203(20)
Invertebrate egg diameter (μm)						
SE Hokkaido	184(133)		114(92)	80(46)	76(74)	117(68)
Joban		160(133)	35(18)	107(83)	85(54)	65(49)
Copepod prosome length (μm)						
SE Hokkaido		1163	525(109)	279(89)		432(117)
Joban	701(231)	541(90)	232(34)	470(130)	715(28)	351(82)

*Mean (standard error)

Table 6-4. Calculated carbon content (μ g C Krill-1) of each indentifiable food item in the stomach contents of *Euphausia pacifica* *

		Diatoms	Dinoflagellates	Tintinnids	Invertebrate eggs	Copepods	Total
SE Hokkaido	Apr.	0.061	0.005	0.011	0.138	0.000	0.215
	Jun.	0.000	0.000	0.002	0.000	3.130	3.133
	Aug.	0.001	0.006	0.056	0.054	1.776	1.893
	Oct.	0.004	0.008	0.034	0.015	0.184	0.246
	Dec.	0.001	0.000	0.020	0.007	0.000	0.027
	Feb.	0.002	0.019	0.156	0.070	1.672	1.933
Joban	Apr.	0.001	0.004	0.002	0.000	4.773	4.781
	Jun.	0.000	0.010	0.003	0.045	7.085	7.143
	Aug.	0.000	0.013	0.001	0.003	0.547	0.567
	Oct.	0.002	0.004	0.000	0.018	5.010	5.035
	Dec.	0.001	0.016	0.001	0.028	2.285	2.331
	Feb.	0.008	0.018	0.010	0.006	0.565	0.608

*Note that carbon content of food items, except copepods of which figure could be estimated from indigested mandible, was considerably underestimated because they were easily broken by digestion.

Table 6-5. Average body carbon, stomach contents carbon, and daily ration of *Euphausia pacifica* of total identifiable bood items and copepods

		Average body C (mg C)	Stomach contents C (μ g C krill^{-1})	Total daily ration (% Body C d^{-1})	Daily ration of copepods (% Body C d^{-1})	Copepod contribution (%)
SE Hokkaido	Apr.'97	3.77	0.21	0.06	0.00	0.0
	Jun.'97	2.92	3.13	0.86	0.86	99.9
	Aug.'97	3.01	1.89	0.56	0.52	93.7
	Oct.'97	3.18	0.25	0.09	0.07	74.7
	Dec.'97	2.13	0.03	0.02	0.00	0.0
	Feb.'98	2.99	1.93	0.78	0.67	86.5
Joban	Apr.'97	2.62	4.78	1.79	1.79	99.8
	Jun.'97	3.33	7.14	1.85	1.84	99.2
	Aug.'97	1.07	0.57	0.49	0.47	96.9
	Oct.'97	1.60	5.04	3.60	3.58	99.5
	Dec.'97	0.90	2.33	3.44	3.37	98.0
	Feb.'98	2.58	0.61	0.28	0.26	92.9

Table 6-6. Ingestion by adult size of *E. pacifica* of copepods estimated by the stomach contents and total foods estimated by carbon budgets necessary for production and metabolism during feeding survey period (313 days) from April 1997 to February 1998

		Biomass of >10mm (mg C) (A)	Daily ration of copepods (% Body C) (B)*1	Daily ingestion of copepods (mg C) (A×B)	Ingestion of copepods from Apr. to Feb. (mg C) (D)*2	Total ingestion from Apr. to Feb. (mg C) (E)	Copepod contribution (D/E)
SE Hokkaido							
	Apr.	123	0.0	0.0			
	Jun.	293	0.9	2.5			
	Aug.	447	0.5	2.3			
	Oct.	595	0.1	0.4			
	Dec.	23	0.0	0.0			
	Feb.	436	0.7	2.9			
					395	5431	7.3%
Sanriku							
	Apr.	439	0.4	1.8			
	Jun.	97	3.1	3.0			
	Aug.	79	2.5	2.0			
	Oct.	106	1.2	1.3			
	Dec.	34	1.7	0.6			
	Feb.	1003	1.1	11.0			
					867	4480	19.3%
Joban							
	Apr.	237	1.8	4.2			
	Jun.	484	1.8	8.9			
	Aug.	59	0.5	0.3			
	Oct.	43	3.6	1.5			
	Dec.	98	3.4	3.3			
	Feb.	398	0.3	1.0			
					1007	3356	30.0%
Entire survey area							
	Apr.	316	0.5	1.7			
	Jun.	278	1.7	4.7			
	Aug.	177	0.9	1.6			
	Oct.	212	0.5	1.1			
	Dec.	49	2.4	1.2			
	Feb.	650	0.9	5.7			
					768	4206	18.2%

*1 Daily ingestion rate of copepods off Sanriku is from Table 3 in Nakagawa *et al.* (2001).

*2 $\sum((CI_j+CI_{j+1})\times d_{j,j+1}/2)$: CI_j is daily ingestion of copepods for jth survey, $d_{j,j+1}$ is days between jth survey and (j+1)th survey.

krill^{-1}). Tintinnids were scarce throughout the year. Invertebrate eggs were abundant in August (1.0 inds krill^{-1}) and December (0.6 inds krill^{-1}). Copepods occurred throughout the year and were abundant in August and October (both 0.8 inds krill^{-1}) but were scarce (0.25 inds krill^{-1}) in February when diatoms were abundant.

Mean total volumes of diatoms, dinoflagellates and tintinnids, mean diameter of invertebrate eggs and mean prosome length of copepods in the stomach of *E. pacifica* varied between months and areas (Table 6-3). Mean total volumes of diatoms off southeastern Hokkaido tended to be higher than those off Joban, but mean total volumes of dinoflagellates off Joban tended to be higher than those off southeastern Hokkaido throughout the year. Mean prosome length of copepods off southeastern Hokkaido (488 μ m) was not significantly smaller than that off Joban (502 μ m) (Mann-Whitney: $P > 0.05$).

Copepods were the dominant food item by carbon content when they occurred in the stomach (Table 6-4). Stomach content carbon off Joban tended to be higher than that off southeastern Hokkaido. Stomach content carbon off Joban was highest in June (7.1 μg) and higher in April and October (both higher than 4 μg). On the other hand, stomach content carbon off southeastern Hokkaido was significantly lower in April, October and December. The low carbon in August off Joban was due to the small mean prosome length of copepods (232 μm) (Table 6-3) despite the high number of copepods in the stomach (Fig. 6-3). On the other hand, the high carbon content in October off southeastern Hokkaido was due to just one copepod with large prosome length (1,163 μm) in the stomach.

The daily ration (% body carbon day^{-1}) off southeastern Hokkaido was less than 1 % and tended to be lower than that off Joban throughout the year (Table 6-5). On the other hand, the daily ration off Joban was high in October (3.6%), December (3.4%).

Discussion

Nakagawa *et al.* (2001) showed that copepods are the most important food item, in terms of carbon, for most of the year in Sanriku waters but *E. pacifica* might have shifted its food preference to the abundant diatoms in spring, rather than feed on copepods whose escape behavior likely costs the euphausiids additional energy expenditure to catch and ingest them. *E. pacifica* tended to consume many diatoms when a high chlorophyll *a* concentration occurred in the surface or subsurface layers but tended to consume large number of copepods when the chlorophyll *a* concentration was low in the total water column both in southeastern Hokkaido and Joban waters (Fig. 6-3). This tendency is well consistent with that of *E. pacifica* off Sanriku (Nakagawa *et al.*, 2001). Therefore, it is suggested that *E. pacifica* flexibly switches the feeding behavior according to ambient food conditions in the wide range off northeastern Japan.

Both the numerical number and carbon of copepods in the stomach of *E. pacifica* off Joban were generally higher than those off southeastern Hokkaido throughout the year (Fig. 6-3 and Table 6-5). Copepods may be a more important food item for *E. pacifica* off Joban where phytoplankton abundance is lower than that off southeastern Hokkaido throughout the year.

Assimilation of adult size (>10mm) of *E. pacifica* during the entire feeding survey period (313 days) was calculated to be 4,562mg C m^{-2} and 2,819mg C m^{-2} off southeastern Hokkaido and Joban, respectively (gross metabolism multiplied by relative contribution of >10mm for each area [see Tables 5-1-5]). Assuming the assimilation efficiency of ingested food to be 0.84 (Lasker, 1966), ingestion by adult *E. pacifica* during the entire feeding survey period was estimated to be 5,431mg C m^{-2} (4,562/0.84) and 3,356mg C m^{-2} (2,819/0.84) off southeastern Hokkaido and Joban, respectively (Table 6-6). On the other hand, ingestion of copepods by adult size *E. pacifica* during the entire feeding survey period is estimated to be 395mg C m^{-2} and 1,007mg C m^{-2} off southeastern Hokkaido and Joban, respectively, using data of the daily ration of copepods (% Body C d^{-1}; Table 6-5) and biomass of adult size (Fig. 5-2) in each month (Table 6-6). Therefore, the copepod contribution to the total food ingestion for adult size of *E. pacifica* is estimated to be 7.3% (395/5,431) and 30.0% (1,007/3,356) off southeastern Hokkaido and Joban, respectively.

Assimilation and ingestion by adult size of *E. pa-*

cifica over the entire feeding survey period (313 days) is estimated to be 4,480 mg C m^{-2} and 3,763 mg C m^{-2}, respectively off Sanriku by using the same calculations as mentioned above (Table 6-6). On the other hand, ingestion by adult size of *E. pacifica* of copepods during the entire feeding survey period off Sanriku is estimated to be 867 mg C m^{-2}, using data of the daily ration by *E. pacifica* of copepods in Table 3 in Nakagawa *et al.* (2001) and biomass of adult size (Fig. 5-2) in each month (Table 6-6). Then, the copepod contribution to the total ingestion during the entire feeding survey period is estimated to be 19.3 % (867/4,480) off Sanriku. Therefore, the importance of copepods as a food item for *E. pacifica* is assumed to increase with the warmer waters.

Several quantitative problems arise by the examination of stomach contents with a dissecting microscope. Phytoplankton cells are broken by mastication and only a small fraction remains intact in the stomach. Gut pigment analysis could help estimate the amount of phytoplankton ingested. Daily ingestion of copepods was calculated by assuming a gut passage time of 1.08 h (Willason and Cox, 1987) in this study. However, different passage times have been reported for phytoplankton and copepods for *E. lucens* (Stuart and Pillar, 1990). So, the gut passage times for major food items by *E. pacifica* have to be determined experimentally in the future. Copepods were suggested to be entirely consumed by *E. pacifica* in this study. However, the copepod *Pseudocalanus sp.* was not entirely consumed by *E. pacifica* in feeding experiments (Ohman, 1984). So, there is a possibility that ingestion of copepods by *E. pacifica* is overestimated by the present method.

In this study, unidentifiable detrial contents were frequently found in the stomachs of *E. pacifica*. They may be organisms without shells such as naked flagellates and ciliates, marine snow, or other digested organisms. The contribution of naked ciliates as a food source of *E. pacifica* cannot be neglected because the biomass ratio of naked ciliates/tintinnids ranged from 3 to 123 in Sanriku waters (Kato, 1995). Nakagawa *et al.* (2004) suggested that *E. pacifica* ingests many naked ciliates and plays a role in linking the microbial food webs to the classical grazing food chains. In addition, Dilling *et al.* (1998) found that *E. pacifica* assimilates natural marine snow with a relatively high efficiency, similar to the values observed when feeding on diatoms. Marine snow, therefore, can be one of the factors that were not included in the calculation of the carbon content of food items.

As mentioned above, *E. pacifica* is found to be able to utilize a wide variety of food sources. This could sustain the continuous spawning (see **Chapter 3**) throughout the year and make *E. pacifica* one of dominant zooplankton species off northeastern Japan. However, it should be noted that the main resources for spawning in the Oyashio area and its frontal area during summer and autumn might not be copepods but phytoplankton and microzooplankton (Fig. 6-3) and ingestion of copepods might be more important foods for small adults in the warmer waters where they can not obtain foods sufficiently in the surface layer during the same seasons.

Chapter 7. General discussion

In this chapter, three key points are discussed from the results obtained in **Chapters 2-6.** First, the significance of the seasonal migration of *Euphausia pacifica* off northeastern Japan is discussed from the point of view of feeding, reproductive maturation and segregation between developmental stages, comparing with the cases in *Euphausia superba.* Secondly, the mechanism of formation of fishing ground in *E. pacifica* in the Sanriku and Joban coastal waters is discussed in relation to its seasonal horizontal and vertical distribution pattern and physical environments. Finally, the impact on the primary and secondary production by *E. pacifica* off northeastern Japan was estimated and is discussed in comparison with *Neocalanus* species.

Significance of seasonal migration of *Euphausia pacifica* off northeastern Japan

It appears that seasonal change in the distribution of adult *Euphausia pacifica* is clearly affected by that of the Oyashio waters off northeastern Japan (Table 3-2; Figs. 3-15-17). The northward shift of the Oyashio waters along with that of the Kuroshio waters during early summer and fall seems to accelerate large adults to shift their distribution toward

more northern, colder waters as mentioned in Chapter 3. However, simultaneously, this shift might provide them with more productive waters where they can select mainly phytoplankton and microzooplankton as food items (Fig. 6-3) which do not require high energy costs to be ingested compared with copepods, along with the reduction of metabolic requirements in the colder conditions (MacLaren, 1963). In addition, Oyashio area during summer and fall, which is the main distributional area for adult *E. pacifica* (Fig. 3-4), provides them with rather favorable feeding conditions partly because predominant macrozooplankton such as *Neocalanus species* are dormant in the Oyashio area during these seasons (Odate, 1994; Tsuda *et al.*, 1999; 2004). These favorable feeding conditions seem to enable adult *E. pacifica* to conduct active copulation and spawning in the Oyashio area during summer and fall (Figs. 3-4, 10 and 11).

Eggs of *E. pacifica* seem to be rather neutrally buoyant because they were generally distributed within 100 m or so in vertical range (Figs. 4-13, 17, 21 and 25). So, eggs of *E. pacifica* liberated in the surface layer could remain to stay and hatch in the warm surface layer in the Oyashio area during summer and fall (Figs. 3-2 and 19). In addition, larval stages also seem to stay throughout the day in the shallow warmer layer by controlling their diurnal vertical migration (Fig. 4-17) and might accelerate their developmental time in the warmer conditions (Ross, 1981). Thus, this summer-fall hatching could accelerate the growth and reduce the mortality during its early developmental stages in the warmer condition and then contribute to maintaining the population of *E. pacifica* off northeastern Japan.

Euphausia superba off the Antarctic Peninsula is suggested to conduct a seasonal migration between the continental shelf area and oceanic waters for spawning (Ichii *et al.*, 1998) and feeding (Ichii *et al.*, 1998; Siegel, 2000). This causes the segregation in horizontal distribution between the developmental stages, which might have a great effect on the reduction of intraspecific competition and parental cannibalism (Siegel, 2000). On the other hand, the segregation in horizontal distribution might be attributable mainly to the difference of suitable temperature range between developmental stages for *Euphausia pacifica* off northeastern Japan. That is to say, spawning and larval stages occur in the warmer side of the distribution of adult (Table 3-2) and segregate their vertical distribution with that of adults by the suitable temperature range (Fig. 4-27) at night when adults mainly feed (Endo, 1981; Ponomareva, 1963). This horizontal and vertical segregation by water temperatures between developmental stages might contribute to the reduction of intraspecific competition and also cannibalism by adults.

On the other hand, when a suitable temperature range overlaps in the total water column between larval stages and adults such as in the coastal waters off Sanriku in spring, copulated females might liberate their eggs in the deeper layers and larval stages might control their diurnal vertical migration to avoid encountering the aggregation of adults (Fig. 4-13).

In conclusion, seasonal change in distribution of adult *E. pacifica* are affected by water temperatures. This might provide adults with favorable feeding condition to realize reproductive maturation after spring and might cause the segregation of the horizontal and the vertical distribution between developmental stages which contributes to reduce the intraspecific competition and also cannibalism by adults.

Characteristics of formation of fishing ground of *E. pacifica*

Kodama (1995a) and Odate (1991) suggested that the fishing ground tend to be formed at the surface temperatures >5℃ because the cold water temperatures <5℃ are not suitable for *E. pacifica* based on empirical data. In March 2001, the fishing ground seemed to be formed avoiding the 0℃ isotherm close to the shore (Fig. 2-18), so such extreme cold temperatures may not be favorable for *E. pacifica*. These cold temperatures may cause *E. pacifica* to migrate southward toward off Sanriku and Joban regions along with the southward advection by the Oyashio Current during late winter and spring, which is well supported by the results in the cylindrical-conical net survey (Figs. 3-15-17). However, the lower limit of suitable temperature range for *E. pacifica* seemed to be much lower than 5℃ from the result in the cylindrical conical net survey (Fig.

3-19). On the other hand, it might be advantageous for spawning adults to migrate toward warmer waters because warm conditions accelerate the development of eggs and larval stages (Ross, 1981; Iguchi and Ikeda, 1994) and might consequently contribute to the reduction of mortality during early stages.

The benthpelagic swarms off Joban were usually formed in the area with high surface temperatures up to 15℃ after early summer (Figs. 2-13, 14 and 17). Fishing conditions of *E. pacifica* have been predicted generally using surface temperatures in Sanriku (Kodama, 1995a) but using benthic temperatures in Joban (Ebisawa, 1995). Because temperatures at daytime depth of adult *E. pacifica* are generally below 8℃ (Figs. 4-7) and its distribution needed lower temperatures <8℃ in the benthic layer in the Sanriku coastal waters (Figs. 4-6 and 7), lower temperatures <8℃ are considered to be necessary for its habitat. Fig. 7-1 shows the seasonal change of average water temperatures at 0, 100 and 200m from January to July throughout 18 years off Nakaminato, Ibaraki Prefecture, one of the main ports. The surface temperatures abruptly rose from May, but the cold waters <8℃ derived from the Oyashio Current intruded at 200m depth from May to June when the fishing grounds are mainly formed in the Joban coastal waters. On the other hand, daytime depth of adult *E. pacifica* is generally above 150m in spring when thermocline is undeveloped and phytoplankton is abundant, but is below 200m from summer to autumn (Figs. 4-13, 17, 21 and 25). Therefore, it is suggested that daytime depth of adults shifts to deepen in early summer. From this evidence, the typical seasonal pattern of formation of fishing ground in the Joban coastal waters is as follows. The distribution of adult *E. pacifica* is blocked by the waters with warmer temperatures >8℃ in the shallow layers, usually located north of Oshika Peninsula (ca. 38°20' N) and is not likely to extend to the Joban coastal waters during late winter and spring. In early summer, however, adult *E. pacifica* shift to deepen its daytime depth below 200m, and then a part of them, whose southward distribution has been blocked by the warmer waters in the shallow layer by early summer, might encounter the cold water mass in the mid-layer, which intrudes toward the Joban coastal waters, during the daytime and be advected southward by this water mass. And then, this advected population may mainly form the fishable benthic swarms in the Joban coastal waters.

Odate (1991) showed that fishing depths in Joban were shallower than 50 m depth from 1981 to 1984 when the southward shift of the Oyashio Current

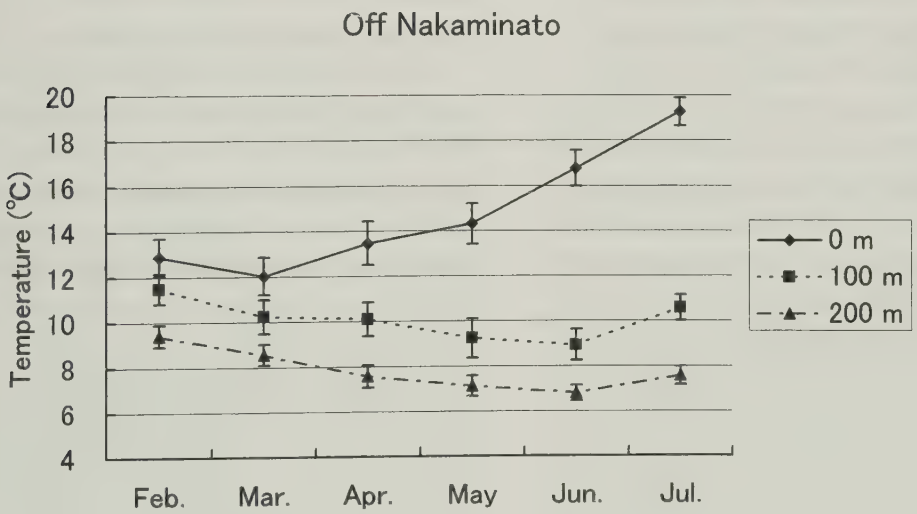

Fig. 7-1. Average temperature (℃) at 0, 100, 200m depth off Nakaminato, Ibaraki Prefecture (36°34' N, 141°04' E).

was strong. The fishing period in these years was significantly earlier than other years (Fig. 2-9). So, it is suggested that adult *E. pacifica* were advected by the surface layer with low temperatures <8 C toward the Joban coastal waters simultaneously to the Sanriku coastal waters during late winter and spring in such strong Oyashio years.

However, it may be difficult for large adults to survive after summer in the benthopelagic form in the warm Joban coastal waters as mentioned above. This is also well supported by the low catch and CPUE after July at Otsu Port (Fig. 2-11).

In conclusion, it is suggested that the fishing ground or fishable aggregations in spring are mainly formed in the cold waters of the transitional area as mentioned in the previous reports perhaps due to the facilitation of copulation, spawning and growth of larval stages in the warmer conditions. On the other hand, the fishing ground in the Joban coastal waters in early summer might be due to the encounter of *E. pacifica* which shift to deepen the daytime depth with the intrusion of cold water mass derived from the Oyashio Current in the mid-layer, and the southward advection of *E. pacifica* toward the Joban coastal waters by this intrusion.

Impact on the primary and secondary productions by ingestion of *E. pacifica* off northeastern Japan

Other than *Euphausia pacifica*, *Neocalanus species* (*N. cristatus*, *N. plumchrus* and *N. flemingeri*) are also the dominant large grazing copepods occurring off northeastern Japan and predominant components of the zooplankton biomass (Conover, 1988; Mackas and Tsuda, 1999; Kobari *et al.*, 2003). Kobari *et al.* (2003) estimated that the annual production and ingestion in carbon in *Neocalanus species* is 19.3 and 38.9 g C m^{-2} in the southeastern Hokkaido region. Therefore, production and carbon ingestion by *E. pacifica* during the survey period (3.8 and 9.1g C m^{-2}) corresponds to about one fifth and one fourth of annual production and ingestion by *Neocalanus species*, respectively, in this region (Table 5-1). Taniguchi (1981) showed that the annual primary production in the subarctic and polar frontal (transitional) area in the northwestern Pacific is 100-150 g and 80-100g C m^{-2}, respectively. Therefore, annual carbon ingestion by *E. pacifica* off southeastern Hokkaido (ca. 9.1g C m^{-2}; Table 5-1) is estimated to correspond to ca. 6-9% of the annual primary production in the subarctic area. While, the annual carbon ingestion by *E. pacifica* off Sanriku and Joban (ca. 9.2 and 6.3g C m^{-2}; Table 5-1) is estimated to correspond to ca. 6-11% of the annual primary production in the polar frontal area.

Carbon ingestion by adult size of *E. pacifica* during the survey period off southeastern Hokkaido, Sanriku and Joban is estimated to be 5.4, 5.1 and 3.4g C m^{-2} (9.1×0.594, 9.2×0.554 and 6.3×0.531; Tables 5-1 and 5), respectively. While, carbon ingestion by adult size of *E. pacifica* of copepods is calculated to correspond to 7.3, 19.3 and 30.0% of the total off southeastern Hokkaido, Sanriku and Joban during the feeding survey (Table 6-6). So, carbon ingestion during the entire survey period off southeastern Hokkaido, Sanriku and Joban is estimated to be 0.4, 0.98 and 1.01g C m^{-2} (5.4×0.073, 5.1×0.193 and 3.4×0.3), respectively. Taniguchi (1981) showed that secondary production in the subarctic and polar frontal area in the northwestern Pacific is 6.0-18.2g and 4.0-10.8g C m^{-2}, respectively. Therefore, the annual carbon ingestion by adult size *E. pacifica* of copepods off southeastern Hokkaido is estimated to correspond to ca. 2-7% of the annual secondary production in the subarctic area. On the other hand, annual carbon ingestion by adult size *E. pacifica* of copepods off Sanriku and Joban is estimated to correspond to ca. 9-25 % of the annual secondary production in the polar frontal area.

If carbon ingestion other than copepods is supplied from phytoplankton, annual carbon ingestion by adult size *E. pacifica* of phytoplankton off southeastern Hokkaido is calculated to correspond to ca. 3-5% of the annual production in the subarctic area. While, if so, annual carbon ingestion by adult size *E. pacifica* of phytoplankton off Sanriku and Joban is calculated to correspond to ca. 2-5% of the annual production in the polar frontal area. So, ingestion impact by adult *E. pacifica* on secondary production is suggested to be rather higher than that on the primary production in the polar frontal area.

In conclusion, annual impact on primary production by adult *E. pacifica* does not seem to be as high as compared to that by *Neocalanus species* in the Oyashio area. On the other hand, ingestion by small

adults might have a significant effect on the secondary production in the transitional area during summer and fall. Conversely, secondary production in the transitional area during summer and fall may sustain the survival of small adults during the same seasons, which could allow their active participation in spawning in the transitional area during the following spring.

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博士号論文

伊豆諸島北部海域におけるタカベの資源学的研究[*1]

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A study on the population dynamics of yellowstriped butterfish in the waters around the northern part of the Izu Islands.

Shingo WATARI[*2]

Abstract The yellowstriped butterfish, *Labracoglossa argentiventris*, inhabit shallow waters over rocky bottoms along the Pacific coast from Kyusyu Island to the Boso Peninsula. This stock is important to coastal commercial fisheries in the northern part of the Izu Islands, which use bulk net, gill net, seine and set net to catch this resource. Assessment and management of the stock are necessary for its effective utilization. This thesis focuses on the population dynamics and stock assessment of yellowstriped butterfish, such as age and growth, standardization of catch per unit effort (CPUE), and abundance estimation, to provide information for fisheries resource management.

In Chapter 2, a method to determine the age of yellowstriped butterfish using from the otolith was studied. The edge of the opaque zones as a ring mark on sectioned sagittal otoliths was used. Monthly changes in the marginal growth rate and proportion of appearance of ring marks on the edge of the otolith were examined. Formation of the first ring was observed during spring or summer, corresponding to one and a half years after hatching. Thereafter, one ring was formed each year in the same season as the previous year.

In Chapter 3, age, growth and maturity were examined using samples collected in the waters around the northern part of the Izu Islands from 1994 to 2003. Age distribution was estimated from the otoliths and scales. Age distribution determined from the scales resulted in an underestimation compared to the values from the otolith analysis. The comparison of multiple age determination indicated that within reader bias of otolith was smaller than that of scale.

Growth was investigated by fitting the von Bertalanffy growth model to the age-length data and the allometric growth model to the length-weight data using maximum likelihood methods. Because the number of small sized fish was insufficient, all parameters could not be estimated by areas (Izu Oshima Island, Toshima Island ～ Shikinejima Island, Kouzushima Island). The selected von Bertalanffy growth model, based on the Akaike Information Criterion (AIC), was the differential asymptotic length and variance by area and sex, and growth coefficient by sex. The growth of yellowstriped butterfish was fast until 2 years of age. The estimated asymptotic length of females was larger than that of males. The estimated asymptotic length in the southern part of the study area was larger than that in the northern part of the study area. The effect of the difference of ageing character, otolith or scale, on the growth curve was investigated. Age before 1 year old fish was determined using the large differences in fork length between the older fish, so ageing character was not used. Because

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the growth speed of large sized fish was slow, age-length relationship was almost same after 4 years of age. For these reasons, difference between the two growth curves was much smaller. The selected allometric growth model, based on the AIC, was multiplicative error structure of differential sex in parameters. The monthly change of the value of Gonadosomatic Index was high from September to December, spawning season, and the peak was October. The maturity rate of 1 year old was 15% and that of after 2 years old was 100%.

In Chapter 4, standardization of CPUE was carried out to improve the reliability of the abundance index. To estimate a year effect, any other factors that may influence CPUE were removed from index by using the generalized linear model. Landing in weight by each operation of gill net of Izu Oshima Island, seine from Toshima Island to Shikinejima Island, and bulk net of Kouzushima Island were obtained from 1991 to 2003 by landing slips. Data of sea surface temperature and current pattern of Kuroshio were also obtained for the same period. Because there was little information about movement in the study area, two hypotheses were considered about the movement after recruitment, the case to move from one island to other islands, and the case that there is no movement among islands. Year, month, area, fishing methods, sea surface temperature, and current pattern of Kuroshio were incorporated as main effects and two-way interactions. For each area, the best model was statistically selected by the AIC from all candidate models. The year effect of standardized CPUE was calculated by least squared mean. The trend of relative abundance of yellowstriped butterfish has remained at the same level after 1991.

In Chapter 5, stock size of yellowstriped butterfish was estimated by the tuning virtual population analysis based on two hypotheses about the movement among islands using the catch at age and CPUE data. The previous study of rearing experiment showed that probability of agreement of true age by using data from otoliths was higher than that from scales. In addition, previous chapter also indicated that within reader bias for otoliths was lower than that for scales. For these reasons, the otolith ageing was considered to be true for catch at age estimation, and the bias in scale ageing was corrected for the basis for otoliths. The standardized CPUE was used as an abundance index for the tuning. Parameters were estimated by the least squares method and standard error was also estimated by the bootstrap method using resampling data of CPUE and catch at age. The yearly change of stock size of yellowstriped butterfish in the northern part of the Izu Islands after 1998 ranged from 600 to 700 metric tons. The catch rate of this stock ranged from 20 to 30%. The estimated standard error of the stock size became larger in recent years. Coefficient of variation of stock size in 2003 was 0.2. The selectivity of older fish was higher than that of younger fish. This result suggests that the target of this fishery is large sized fish which are high priced, and fishing intensity of small sized fish is low. The estimated stock size, fishing mortality, and selectivity, using two hypotheses of the movement shows the same trends. A similar conclusion of the stock management plan was possible. The percent spawning per recruitment was about 50% in 2003 in each area. The results showed that if the fishing effort is increased from the present level, the amount of catch of large sized fish would decrease, although the total amount of catch would
increase slightly.

The present level of fishing mortality is close to F0.1. Yield per recruit and spawning per recruitment analysis also suggested that the current level of exploitation is not overfishing. For the sustainable use of yellowstriped butterfish stock, both the current level of fishing effort and low fishing intensity on younger fish should be maintained.

Key words: yellowstriped butterfish, age, growth, otolith, abundance estimation

目　次

第一章　緒　　論
第二章　耳石による年齢査定
第三章　年齢・成長・成熟
第四章　単位努力量あたり漁獲量の標準化
第五章　資源量推定
第六章　総合考察
謝　辞
文　献
Appendix A

第一章　緒　　論

我が国において水産業は食糧を供給し，地域経済を支える産業として重要であるが，資源水準の悪化や漁業者の高齢化など多くの問題を抱えている。資源水準を維持，回復する目的で，全国各地の様々な魚種において資源管理が実施されている。東京都の伊豆諸島においても，水産業は地域の経済を支える持続可能な産業として重要であり，資源管理が積極的に推進されている。平成13年度からハマトビウオ *Cypselurus pinnatibarbatus* について生物学的漁獲許容量に基づく数量管理が実施され，タカベ *Labracoglossa argentiventris* やキンメダイ *Beryx splendens* などについても資源解析の必要性が指摘されている。タカベは，伊豆諸島北部海域において，2003年の水揚げ重量，金額ともに1位の主要漁獲物である。当資源の有効利用を図ることは，地域の水産業においても重要な課題である。資源管理の方策を決定するには，対象となる資源生物の年齢や成長，成熟，漁獲量，努力量など，様々な情報が必要となる（Hilborn and Walters, 1992; Quinn and Deriso, 1999）。タカベに関する調査研究は，東京都水産試験場（現東京都島しょ農林水産総合センター）による地先・沖合定線調査や，卵稚仔，幼魚期の研究（服部，1964；小達，1962；武藤，1970），年齢や成長の研究（有馬，1984；安藤ら，2004），漁業と海況の関係の研究（有馬，1982；有馬，1986；有馬，1995）などがある。しかしながら，年齢と成長や，漁業と海況の関係については，まだ不明な点も多い上，資源の現状評価も不十分である。タカベ資源の持続的利用を確保するため，資源学的研究を推進する必要がある。

タカベの生物学的特性

タカベは，スズキ目タカベ科タカベ属の1科1属1種の魚種である。生息域は，房総半島から九州にかけての太平洋岸の外洋に面した岩礁地帯で日本沿岸に限られる。伊豆諸島では大島から八丈島周辺の水深50m以浅に分布すると考えられ，利島から神津島がその中心である（Fig. 1.1）。体色は，背部が青緑色がかっており腹部が銀色で，背部から尾部にかけての側線付近に黄色の帯がある。動物性プランクトンを捕食し，コペポーダを主食としている。

タカベの産卵期は秋で，生殖腺の熟度指数は9月末から10月にかけて上昇し，11月まで他の時期と比較して高い値を示す（有馬，1984）。飼育環境下においても，産卵は天然と同じ10～12月に観察され，1月以降観察されていない（有馬，1999）。仔稚魚は，10月以降伊豆諸島周辺海域おいて広範囲に分布しており（武藤，

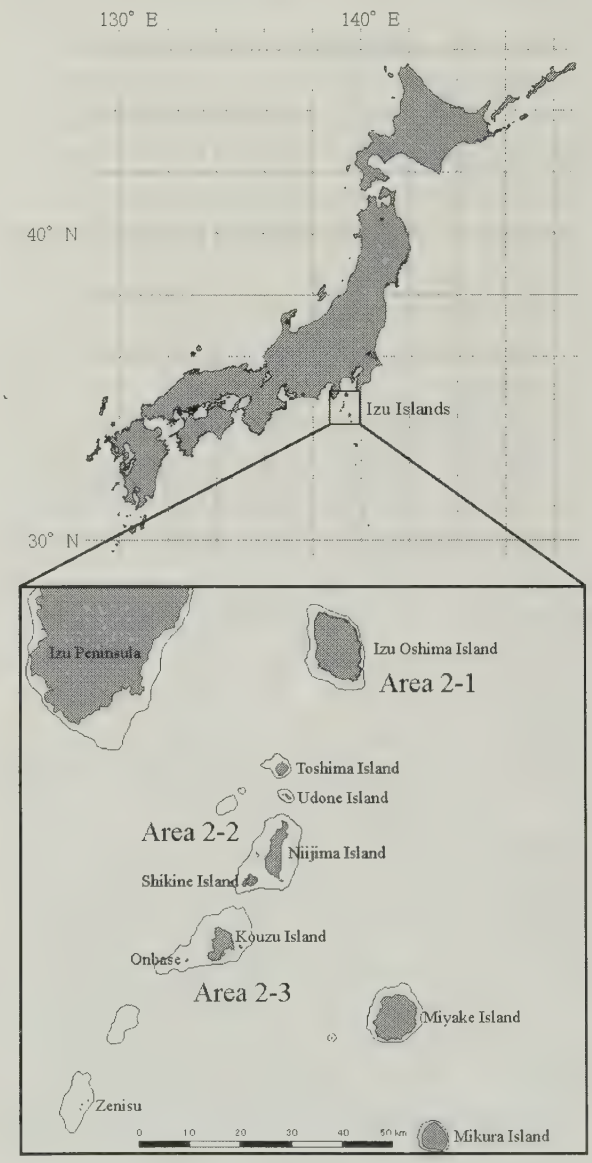

Fig. 1.1. Location of the study area. The depth contour shows 100m in depth.

1970)，翌春から小型魚（通称ムギタオシ）が大島～八丈島周辺の水深40m以浅の岩礁域に出現する。成魚は春から秋にかけて岩礁地帯に群で観察されるが，冬期はより深いところに生息すると考えられている。生息に適した水温は17～25℃で，16℃を下回ると摂餌が不活発となり成長が止まる（有馬，1984)。

東京都水産試験場資源管理部(2004)によると，大島，新島，式根島，神津島で採集された個体のミトコンドリアDNAのD-roopのハプロタイプの出現頻度を比較したところ，島間で有意な差は検出されなかった。また，仔稚魚が産卵期直後に伊豆諸島周辺海域の広範囲で観察されることから，各島周辺で生まれた個体は混ざり合い，1つの系群であると考えられる。しかし，大島，利島，鵜渡根島，新島，神津島において，1982～2002年の間に実施された標識放流実験では，4,521個体放流され，160個体再捕報告があったが，いずれの再捕報告も放流した島内であり，別の島へ移動した報告はなかった。また，有馬（1990）は島間で成長に差があり，隣の島でも同一年齢の尾叉長の平均値が異なることを報告している。伊豆諸島の各島は，ほとんどが火山島で，各島周辺の水深が急激に深くなる。そのため，岩礁域に生息するタカベが，加入以降どの程度，範囲で移動するか十分に解明されていない。

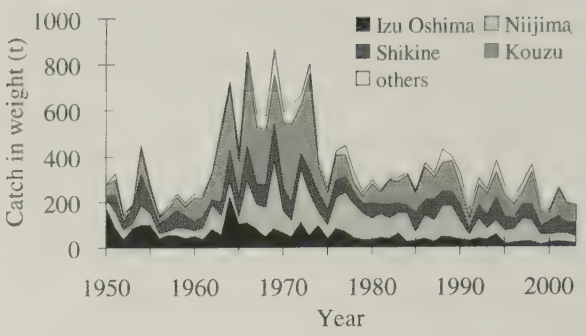

Fig. 1.2. Yield of yellowstriped butterfish in the Izu Islands from 1950 to 2003.

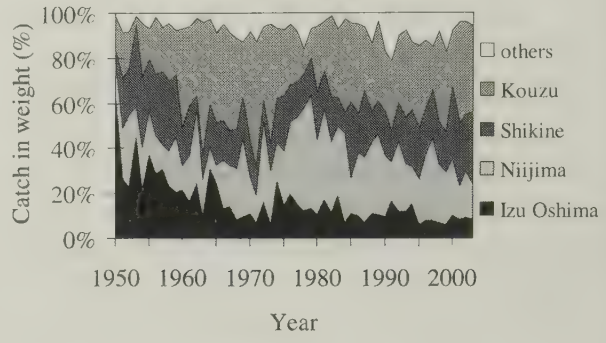

Fig. 1.3. Proportion of yield of yellowstriped butterfish in the Izu Islands from 1950 to 2003.

タカベの漁業

タカベは伊豆諸島において古くから利用されており，室町時代には貢租として現物で上納され，また，江戸時代には干物が江戸へ出荷されていた（東京都水産試験場，1984)。タカベの盛漁期は夏で魚体中に脂が多く含まれるため，冷蔵保存設備が不十分であった戦前戦中まで，鮮魚で島外に出荷されることは少なかった。タカベの漁獲が盛んになったのは戦後で，東京都の漁獲統計資料によると，伊豆諸島海域における年間漁獲重量は，1950年代に200t前後を推移していたが，1960年代と1970年代前半にかけて年間700t前後に増加した。1969年には戦後最高の869tに達した。しかし，1974年以降漁獲量は減少し，1980年代は年間300t台，1990年代からは年間200t前後を推移している。1950～2003年までの伊豆諸島全体の漁獲量（t）の経年変動と島別漁獲割合をFig. 1.2, Fig. 1.3にそれぞれ示す。

伊豆諸島周辺海域では，現在，建切網，寄網，刺網，定置網の4種類の漁法で漁獲されている。以前，4そう張網，2そうまきあぐり巾着網も同海域で操業していたが，現在は行われていない（有馬，1982)。建切網と寄網は，総勢40～50名ほどの漁業者が十数隻の漁船を使用し，潜水でタカベ魚群を追い込み一気に巻いて漁獲する大規模な漁法である（東京都水産試験場，1975；東京都水産試験場大島分場，1994)。両者はタカベやイサキを主に漁獲し，他にもカンパチ，シマアジ，ヒラマサ，マダイなども漁獲する。最盛期には建切網が神津島で5ヵ統，寄網が伊豆諸島全域で8ヵ統操業していたが，現在，建切網が神津島で1ヵ統，寄網が新島若郷で1ヵ統が操業しているのみである。刺網は伊豆諸島北部海域の各島で操業しており，中でも式根島での漁獲量が多く，同島だけで伊豆諸島海域のタカベ漁獲量の4分の1近くを漁獲している。刺網，建切網，寄網漁業は第二種共同漁業権に基づいて行われている。漁業権は大島周辺海域，利島周辺海域，新島と式根島周辺海域，神津島周辺海域にそれぞれ設定されている。また，水産資源の保護を目的として東京都漁業調整規則により全長100mm未満のタカベの採捕が禁止されている。

本研究の目的

本研究は，大島から神津島に至る伊豆諸島北部海域において，タカベ資源の現状評価を行い，資源管理に必要な基礎的情報を得ることを目的とする。同海域の各島から，資源解析の基礎となる年齢や成長，成熟について調査し，漁獲量，努力量の情報を収集した。本論文では，耳石による年齢査定，年齢・成長・成熟，

CPUEの標準化，資源量推定と現状評価について4つの章に分けて議論した。

第二章では，従来年齢査定に使用されていなかった耳石について，年齢形質としての有効性を検証した。伊豆大島周辺海域で収集したタカベの耳石の不透明帯の外縁を輪紋として，縁辺部の輪紋出現割合と縁辺成長率から輪紋形成時期を調べた。

第三章では，年齢，成長，成熟など資源解析および管理の基礎となる生物学的情報について調べた。耳石と鱗を使用して年別地区別漁法別の輪紋数組成を調べるとともに，両者の輪紋数の関係を比較した。輪紋数査定値の信頼性の評価するため，読み取り誤差の評価も行った。また，年齢と成長の関係を把握するため，年齢－尾叉長関係のvon Bertalanffy成長式と，尾叉長－体重関係のアロメトリー式を推定した。さらに，雌雄の年齢別成熟率と成熟サイズについても調べた。

第四章ではCPUEに含まれる年変動以外の要因を取り除き，資源量指数としての信頼性を高めるため，一般化線形モデルを使用し標準化を行った。年，月，場所と，黒潮や水温などの環境要因の主効果と，その交互作用に分離し，年変動のみを抽出した。

第五章では，第三章で得られた年齢と，第四章で得られたCPUE，年別地区別の漁獲量を用いて，資源の絶対量をチューニングVPAで推定した。資源量推定結果から漁獲割合や年齢ごとの選択率など，漁獲の現状評価を行った。また，YPR，SPR解析を行い，現在の漁獲圧とそれが変化させた場合の影響についても評価した。

第二章　耳石による年齢査定

魚類の年齢を調べる方法には年齢形質法，体長組成法，飼育法，標識放流法など様々なものがある（久保，吉原，1969；能勢ら，1988；DeVries and Frie, 1996）。タカベの年齢査定に関する研究は，鱗を用いた年齢形質法と飼育法が行われている。有馬(1984)は，伊豆諸島周辺海域のタカベの鱗の断切部を輪紋とし，生後1年半の4月ごろに第1輪が形成され，その後1年に1本ずつ輪紋が形成されること示した。この結果をもとにタカベの年齢査定は，従来鱗を使用して行われてきたが，輪紋の読みにくさや，精度の悪さが指摘されている（東京都水産試験場, 2000）。安藤ら（2004）は，生後半年の小型魚を27ヶ月間飼育した結果から，耳石と鱗の第1輪が生後1年半で形成され，第2輪が翌年の同じ時期に形成されると報告している。しかし，年齢と輪紋数の関係は，耳石の場合完全に一致するものの，鱗の場合若齢であっても輪紋数がばらつくことから，輪紋形成が不安定であることを指摘している。このため，天然個体において鱗に変わる年齢形質の使用が検討されている。本章では，伊豆大島周辺海域で収集したタカベの耳石を使用し，年齢形質としての有効性を示す。

試料と方法

試　料

耳石の年齢形質としての有効性を調べるため，2000年5月から2003年10月にかけて伊豆大島周辺海域で合計1,357個体を収集した（Group 1）。標本は調査（タモ網（Group 1-A），釣り（Group 1-D））と，漁業（刺網（Group 1-B），定置網（Group 1-C））で捕獲した（Table 2.1）。

方　法

標本は測定まで冷蔵保存し，尾叉長を定規を使用し1 mm単位で計測した。体重と生殖腺重量は電子天秤を使用して，それぞれ1 g，0.01g単位で計測した。性別は生殖腺を目視で観察し，雄，雌，性別不明に分類した。精巣はクリーム色で産卵時期に乳白色になり膨らむ。卵巣は表面に血管が見られ赤みがかっており，産卵時期に黄白色の卵が観察できる。魚体測定後，頭部から耳石（偏平石）を摘出した。Group 1-B, C, Dの標本から摘出した耳石は，水道水に数日間浸し，その後99.5%のエチルアルコールに浸し，乾燥させマイクロプレートに保存した。Group 1-Aの標本から摘出した耳石は，70%エチルアルコールに浸して保存した。

耳石の構造が湾曲しており表面から輪紋を適切に観察出来なかったので，切片を作成した。耳石をポリエステル樹脂で包埋し，核をはさむように横断方向にダイヤモンドカッターを用いて切断した。そして，スライドガラスに貼り付け，核が明瞭に見えるまで研磨紙（600－2,000番）で磨いた。切片の厚さは約0.5mmであった。

耳石の切片は顕微鏡の透過光を使用し40倍で観察した。切片の表面を見ると，耳石の成長方向が変化する狭い不透明帯が観察できた。この不透明帯の外縁を年輪として使用し，その輪紋数を計測した(Fig. 2.1b, c)。輪紋数を計測する際，査定者には尾叉長，体重など魚体の情報を与えなかった。

耳石の成長方向は，Fig. 2.2のように変化している。耳石長は隣りあう輪紋の距離を腹側から背側まで核を経由して計測した。距離の計測はパソコンで耳石のデジタルカメラ画像を使用した。

輪紋形成時期を特定するため，月ごとの縁辺部の輪

Table 2.1. Samples collected for age validation using otolith from 2000 to 2003 around Izu Oshima island.

Date	Number of samples (male : female : unknown)	Fork length (mm)	Fishing (sampling) gear	Group
2000				
29 May	15(0:0:15)	65-81	brail net	1-A
19 Jun	7(0:0:7)	78-90	brail net	1-A
2001				
25 Jul	158(83:75:0)	167-210	gill net	1-B
19 Oct	121(65:56:0)	162-209	set net	1-C
8 Nov	158(93:65:0)	168-211	gill net	1-B
11 Dec	124(76:48:0)	161-208	set net	1-C
2002				
5 Apr	90(44:46:0)	150-204	set net	1-C
19 May	84(43:41:0)	166-212	gill net	1-B
14 Jun	152(72:80:0)	161-203	gill net	1-B
26 Jul	116(56:53:7)	145-207	gill net	1-B
4 Sep	185(106:79:0)	155-201	gill net	1-B
2003				
15 Oct	117(59:51:7)	111-144	angling	1-D
16 Oct	30(14:10:6)	114-135	angling	1-D

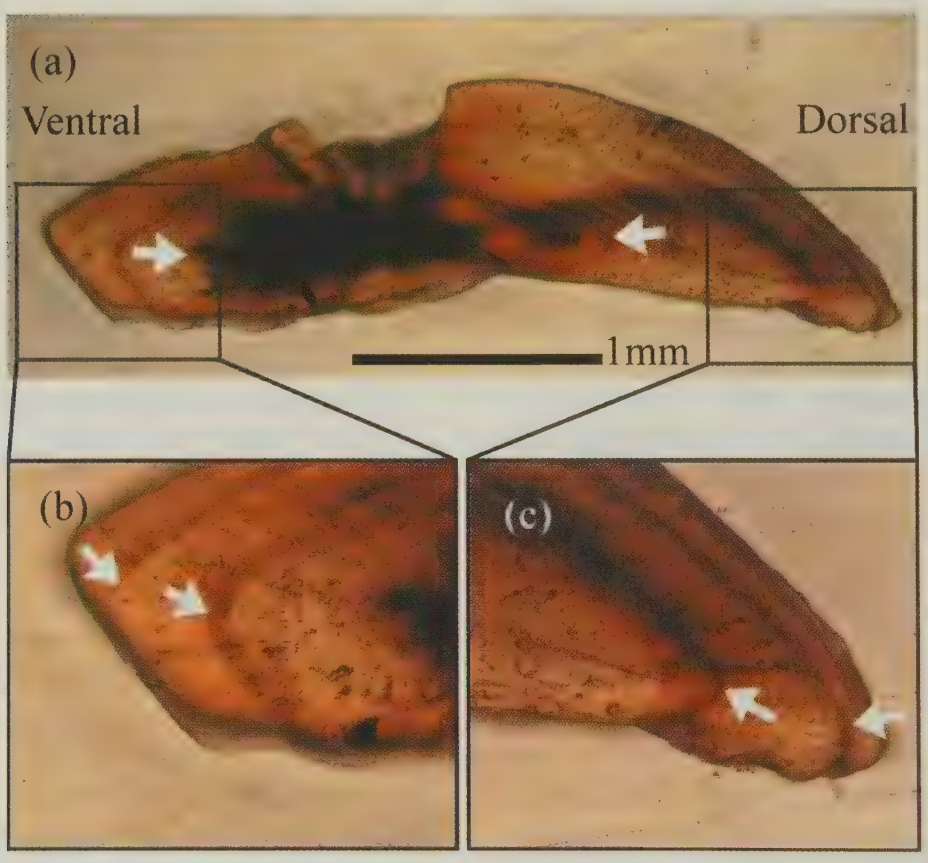

Fig. 2.1. A sectioned otolith of butterfish. (a) A typical overlook (x 40) and irregular ring (arrowhead). (b) and (c) Detailed views of both the dorsal and ventral side (x 200). The arrowhead indicates the annual rings.

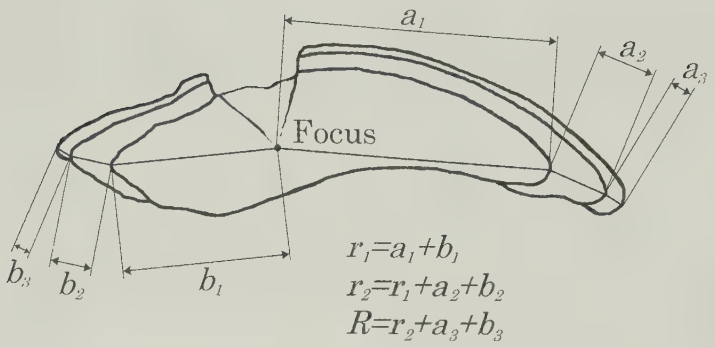

Fig. 2.2. An example of measurement of an otolith. Notations "R" and "r_n (n=1,2)" indicate the whole diameter and diameter at ring formation.

紋出現割合と縁辺成長率を求めた。耳石の縁辺部の状態は以下の3つに分類し，全体のうち(i)の占める割合を縁辺部の輪紋出現割合とした。

(i) 耳石の縁辺に輪紋が形成した直後
(ii) 耳石の縁辺に輪紋が形成していない
(iii) 耳石とポリエステル樹脂の接着面の乱反射のため縁辺の状態が観察できない

縁辺成長率は，耳石長から以下の式で求めた。

$$\text{縁辺成長率} = \frac{R - r_n}{r_n - r_{n-1}} \qquad (2.1)$$

ここで，R (mm) は全径，r_n (mm) は核から外側に数えて n 番目の輪紋までの長さを示す。尾叉長 (FL) と R の関係の対数線形式を最小2乗法で求めた。また，その関係式から輪紋形成時の尾叉長の理論値を求めた。第1輪形成時期を調べるため，耳石に輪紋が形成されていない小型魚の年齢は，過去に行われた仔稚魚調査結果の月ごとの尾叉長組成データを使用して決定した（小達，1962；武藤，1970；有馬，1984)。

結　　果

Group 1の耳石の輪紋は1,357個体中1,351個体を計測することができた（可読率 =0.996)。6個体の耳石は輪紋が不明瞭なため，輪紋数を計測することが出来なかった。耳石の計測可能個体のうち，尾叉長145～212mm の1,182個体には1～7本の輪紋が形成されていたが，尾叉長65～144mm の169個体には輪紋が形成されていなかった。輪紋が形成されている個体のうち3.7% は，耳石の一部が破損しているため，耳石長を計測することが出来なかった。また，耳石の可読個体うち32% には，第1輪の内側に偽輪が形成されていた（Fig. 2.1a)。雌雄は Group 1-B, C, D の1,315個体で判定できた。雄，雌，性別不明の個体数はそれぞれ，711，604，42個体だった。Group 1-A の性別は生殖腺が小さいため判定できなかった。

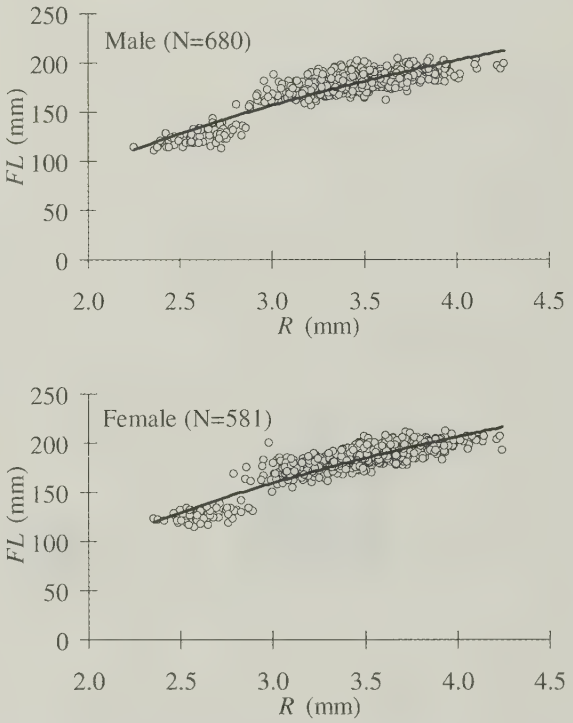

Fig. 2.3. Relationship between whole diameter (R) and fork length (FL). The open circles and curves show the data and esti) mated ones.

Fig. 2.3は耳石長と尾叉長の関係図である。耳石長と尾叉長関係の対数線形式は，

$FL = 157.73Ln(R) - 16.17$ (雄：$R^2 = 0.79$) (2.2)

$FL = 163.19Ln(R) - 19.98$ (雌：$R^2 = 0.80$) (2.3)

である。Table 2.2は n 番目の輪紋形成時の尾叉長の推定値である。輪紋形成時の尾叉長の推定値は輪紋数が増加すると，わずかに減少していることを示す。

Table 2.2. Back-calculated fork length (FL_n, mm) at each ring group

Sex	Ring group	Sample size	FL_1	FL_2	FL_3	FL_4	FL_5	FL_6	FL_7
Male	1	96	147						
	2	178	146	169					
	3	207	145	169	178				
	4	96	146	169	178	184			
	5	26	146	167	177	184	189		
	6	7	143	163	174	181	188	193	
	Average		146	169	178	184	189	193	
	Total	610							
Female	1	113	150						
	2	157	149	172					
	3	144	150	173	183				
	4	80	151	176	185	191			
	5	24	148	169	180	188	194		
	6	3	135	159	170	180	186	192	
	7	1	150	169	176	183	188	193	197
	Average		150	173	183	190	193	192	197
	Total	522							

n, number of rings

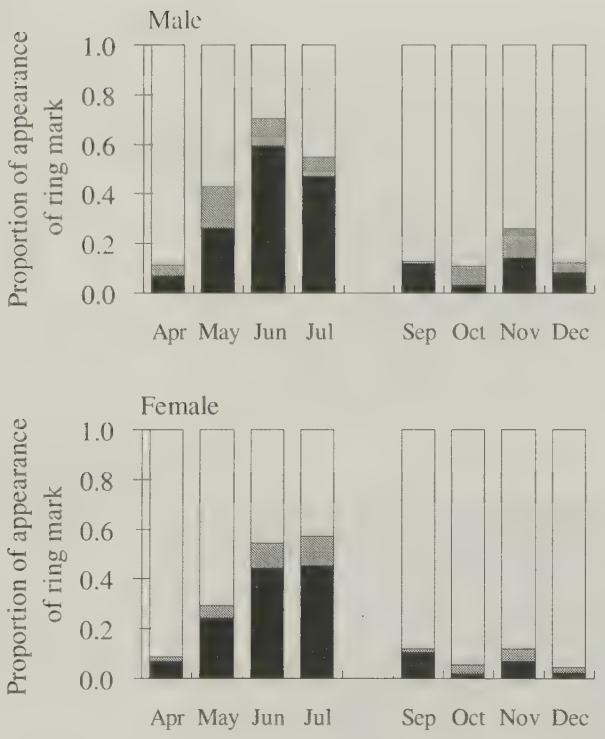

Fig. 2.4. Monthly changes in the proportion of appearance of ring marks on the outer margins of otoliths. The black, white, and gray areas indicate the proportions of ring appearance, no appearance, and unreadable, respectively.

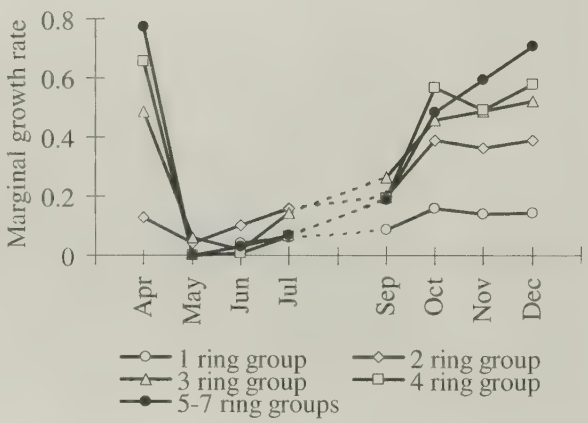

Fig. 2.5. Monthly changes in marginal growth rates of otoliths by ring group

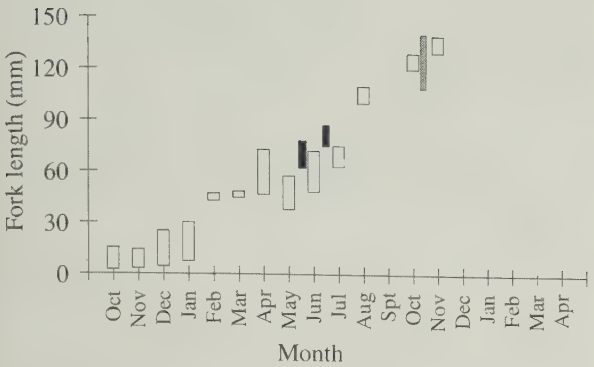

Fig. 2.6. Comparison of monthly changes in fork length frequency distribution. The black, gray, and white bars indicate samples of Group 1-A, Group 1-D, and the past study, respectively.

耳石の縁辺部の輪紋出現割合と縁辺成長率の月変化をFig. 2.4とFig. 2.5にそれぞれ示す。4月から6月にかけて，縁辺部の輪紋出現割合は増加し，縁辺成長率は減少している。このことから，輪紋は1年に1本春から夏にかけて形成され，そのピークが5月と6月であると判断した。この時期の縁辺部の輪紋の計測は，新しい輪紋が形成されていると判断できる個体のみ測定した。ちょうど輪紋が形成されている個体の縁辺成長率は0とした。

年齢を求める際に，10月から11月にかけて産卵期であることから，誕生日を11月1日と仮定した（有馬，1984）。Fig. 2.6は，耳石の輪紋が形成されていないGroup 1-AとGroup 1-Dの尾叉長の範囲と，過去の研究で採集された小型魚の各月の尾叉長の範囲を比較した図である。過去の調査の尾叉長組成と比較すると，Group 1-AとGroup 1-Dの標本は，それぞれ0.5歳と1歳の範囲と一致する。さらに，月と尾叉長組成の関係から，第1輪形成時の推定尾叉長150mm（Table 2.2）に達するのは，翌春の1.5歳であると判断した。

考　察

耳石による年齢査定には，偏平石の切片を作成する以外にも様々な方法がある（Secor *et al.*, 1992）。本研究に先立ち，礫石と星状石の年齢形質としての使用可能性に加え，偏平石の観察方法についても複数検討した。礫石では，表面，切片の観察のいずれにおいても，年輪や日周輪と考えられる周期輪がみられなかった。星状石では，表面観察で周期輪と考えられる輪紋が観察できなかったが，横断方向に切断後，核が切片表面に現れるまで研磨し，10%HClでエッチングを行い，表面を走査型電子顕微鏡で観察したところ，核から縁辺部にかけて300～500本ほどの間隔が密な輪紋が確認できた。この輪紋の観察は非常に手間がかかるため，本研究では年齢形質としての有効性の検証を行わなかった。しかし，今後飼育個体を使用した実験などを行い周期輪であることが確認できれば，年や地域による初期成長の違いの検討など，詳細な解析を行えるかもしれない。また，偏平石を表面観察した場合，高齢になるに従い輪紋が湾曲して形成され間隔が密になり判読しにくくなるため，輪紋の観察方法として不適と判断した。表面法による耳石の輪紋数査定結果は，輪紋の形成方向が変化するため，切片による査定と比較して年齢が過小推定になることがある（Beamish, 1979；Newman *et al.*, 2000）。偏平石の構造を考慮すると，横断方向に切片を作成することは，輪紋数をより正確に計測できる方法と考えられる。

輪紋が形成されていない小型魚の年齢は，尾叉長組成の差を用いて他の年齢群と分離し決定した。耳石と鱗の第1輪輪紋形成前の年齢については，脊椎骨や棘など他の年齢形質を使用することで，査定可能かもしれない。しかし，漁獲対象サイズと比較し小型魚は成長が早いため，尾叉長組成の比較のみで十分に年齢分解が可能である。

輪紋形成時の尾叉長の理論値は，輪紋数が増加するとわずかに減少する傾向が見られる。この原因について，Lee現象と年齢査定誤差の2つの可能性が考えられる。統計的な検定を行っていないが，輪紋数が5本以下のサンプル数は十分にあり，輪紋形成時の推定尾叉長も，各グループ間で非常に近い値であることから，年齢査定誤差とは考えにくい。

耳石を観察した結果32%の個体で，第1輪と核の間に偽輪が形成されていた。この偽輪を誤って輪紋として計測すると，年齢査定において重大な誤差の原因となる。偽輪は通常の第1輪が形成される長さの半分ほどの位置に出現していた。核からの距離の差を利用することで，偽輪と通常輪を区別することは可能である。

有馬（1984）によると，鱗の輪紋形成時期は4月で，本研究結果の耳石の輪紋形成時期とほぼ一致する。冬場の水温が16℃以下になると飼育では成長が停滞することから，鱗の輪紋形成が冬季の成長停滞期から，春季の成長開始期への変化が原因で起こることを示唆している。タカベの耳石の輪紋形成要因も，鱗と共通で，成長の停滞期から開始期への移行によるものと考えられる。

第三章 年齢・成長・成熟

資源生物の年齢，成長，成熟を知ることは資源解析の課題の1つで，成長生残モデルを使用し解析を行うときに必要な情報である（田中，1998；Quinn and Deriso, 1999）。伊豆諸島北部海域において，東京都水産試験場がタカベの生物学的情報を得るため，長期間魚体の収集が行われている。このうち，年齢形質については，近年耳石と鱗両方を収集しているが，2000年以前は鱗の標本しか収集していない。このため，長期間の年齢と成長に関する情報を得るためには，耳石と鱗のデータを併用する必要があるが，天然個体において耳石と鱗の輪紋の関係について十分な把握がなされていない。本章は，耳石と鱗の年齢形質としての関係を把握した上で，年齢，成長，成熟など資源解析に必要な生物学的情報を得ることを目的とする。1994～2003年に伊豆諸島北部海域で収集した標本の耳石と鱗を使用し，年別地区別漁法別の輪紋数組成を調べた。輪紋査定値の信頼性の評価するため，年齢読み取り誤差の評価も行った。また，年齢と成長の関係を把握するため，年齢－尾叉長関係の von Bertalanffy 成長式と，尾叉長－体重関係のアロメトリー式を推定した。さらに，雌雄の年齢別成熟率と成熟サイズについても調べた。

試料と方法

試　料

伊豆諸島北部海域のタカベの年齢，成長，成熟を調べるため，1994～2003年に Group 1の標本も含めた16,932個体を収集した。標本は，漁業（定置網，刺網，寄網，建切網）で捕獲したものが15,382個体で，調査（釣り，たも網）で捕獲したものが1,550個体である（Table 3.1）。

標本は第二章と同様に測定まで冷蔵保存し，全個体の尾叉長と体重，15,289個体の生殖腺重量を計測した。性別は生殖腺を摘出時に目視で観察し，雄，雌，不明に分類した。さらに，15,212個体の鱗を採取し，そのうち1,842個体について頭部から耳石も摘出した。ここで，標本は耳石と鱗の摘出に関して以下の4種類に分類できる。

Group 1　耳石と鱗を摘出し，第二章で耳石の年齢形質としての有効性を調べるために使用した標本（1,357個体）

Group 2　耳石と鱗を摘出した Group 1以外の標本（485個体）

Group 3　鱗のみを摘出した標本（13,352個体）

Group 4　耳石と鱗いずれも摘出していない標本（1,738個体）

輪紋数の計測

1．耳石と鱗の輪紋数査定

Group 1, 2の全個体と Group 3の9,621個体の鱗の輪紋数を計測した。鱗は魚体測定時に，体側の胸鰭の内側から左右約20枚，合計40枚ほど採取し，水道水に半日浸漬した後，5％水酸化ナトリウム水溶液に浸すか，超音波洗浄器に20～30分間入れる，どちらかの方法で表面に付着した細かい組織片などを除去した。その後，水道水ですすぎ，2枚のスライドガラスの間に鱗をはさみ，セロハンテープで接着した。鱗は顕微鏡の透過光を使用して40倍で観察し，輪紋が明瞭に観察できる個体と不明瞭で観察できない個体に分類した。輪紋が明瞭な個体について，有馬（1984）に従い鱗の断切部の輪紋数を計測した（Fig. 3.1(b)）。輪紋数は，査定者に尾叉長や体重など魚体の情報を与えず計測した。また，Group 2の標本の耳石は，第二章で輪紋数を計測した Group 1と同様の方法で計測した。Group 1, 2の標本を使用し耳石と鱗の輪紋数ごとの出現頻度を比較

Table 3.1. Samples collected for age estimation by fishing gear, area and year.

Year	Area 2-1 Gill net	Area 2-1 Set net	Area 2-2 Seine	Area 2-2 Gill net	Area 2-3 Bulk net	Area 2-1 & 2-3 Survey
1994	167	250	0	220	168	0
1995	580	0	67	79	228	61
1996	141	54	0	0	385	129
1997	357	0	0	147	721	1098
1998	92	43	74	284	517	0
1999	71	412	503	284	353	0
2000	526	518	185	751	845	115
2001	812	594	383	713	794	0
2002	589	115	0	381	466	0
2003	341	184	489	198	319	147

した。輪紋数から年齢への変換は，第二章と同様に11月1日を誕生日と仮定した。

2．耳石と鱗の輪紋数査定値の信頼性の評価

耳石と鱗の輪紋を同一査定者が計測したときの査定値の信頼性を調べるため，読み取り誤差の評価を行った。Group 2の319個体について耳石と鱗の輪紋数をそれぞれ1ヶ月おきに3回査定した。輪紋数の読み取り誤差の評価には，3回いずれも査定できた個体のみを使用し，真の輪紋数 h 本（h =1,…, H）に対する，輪紋数観測値 ϕ 本（1, …, Φ_h）の出現確率 $p(\phi|h)$ を推定した。$p(\phi|h)$ は，真の輪紋数が h 本の i 番目（i =1, …, I_h）の個体を合計 $x_{h,i}$ 回の査定したとき，観測値 ϕ 本の出現回数 $x(\phi)_{h,i}$ が多項分布に従うモデルを仮定し推定した。尤度関数は，

$$L=\prod_{h=1}^{H}\prod_{i=1}^{I_h}x_{h,i}!\prod_{\phi=1}^{\Phi_h}\frac{p(\phi|h)^{x(\phi)_{h,i}}}{x(\phi)_{h,i}!} \qquad (3.1)$$

$$\text{但し } x_{h,i}=\sum_{\phi=1}^{\Phi_h}x(\phi)_{h,i}$$

となる。ここで，読み取り誤差の評価において，耳石と鱗それぞれの i 番目の個体の真の輪紋数 h 本は，複数回査定した輪紋数観測値の平均を四捨五入した整数値 h'^{oto} 本，h'^{scl} 本とした。耳石と鱗の輪紋数観測値をそれぞれ，ϕ^{oto} 本，ϕ^{scl} 本とし，$p(\phi^{oto}|h'^{oto})$ と $p(\phi^{scl}|h'^{scl})$ を推定した。

成長式の推定

1．年齢－尾叉長の von Bertalanffy 成長式

性別（s = m, f, u），場所（b = 1, 2, 3）における a

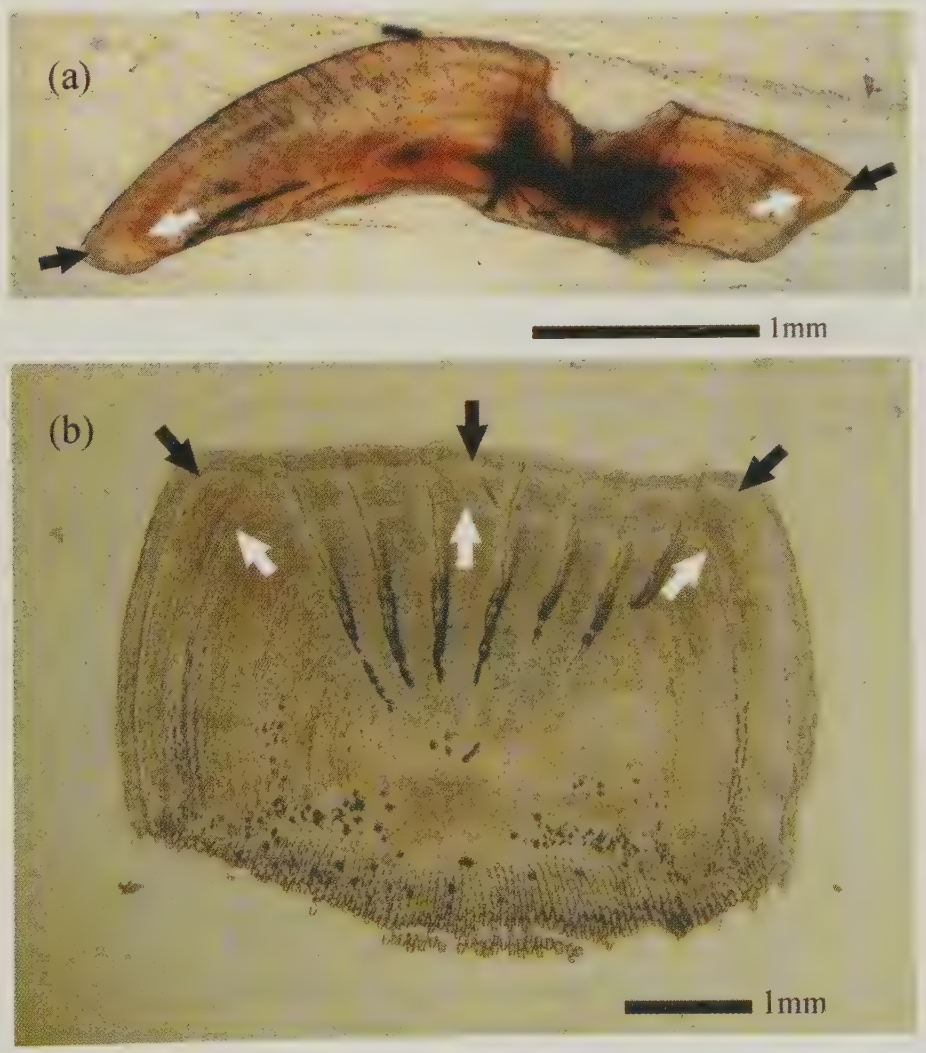

Fig. 3.1. Comparison of the annual rings between otolith (a) and scale (b) of butterfish. The white and black allows indicate first and second rings, respectively.

歳（$a = 0, \cdots, A$）の i 番目（$i = 1, \cdots, I_{s,b,a}$）の個体の尾叉長を $l_{\quad}$（mm）とおく。場所は漁業の操業範囲から b=1, 2, 3に分離し，それぞれ大島周辺海域（Area 2-1），利島から式根島周辺海域（Area 2-2），神津島周辺海域（Area 2-3）とした（Fig. 1.1）。性別 "m", "f", "u" はそれぞれ雄，雌，性別不明を表す。実年齢を $t_{\quad}$（年）と置き，$l_{s,b,a,i}$ を以下のモデルで示す。

$$l_{s,b,a,i} = \hat{l}_{s,b}(t_{s,b,a,i}) + \varepsilon_{s,b,a,i} \qquad (3.2)$$

ここで $\varepsilon_{\quad}$ は平均0，分散 $\sigma^2_{\quad}$（mm^2）の正規分布に従う誤差，$\hat{l}_{s,b}(t_{s,b,a,i})$ は $t_{s,b,a,i}$ 歳における尾叉長の理論値である。$\hat{l}_{s,b}(t_{s,b,a,i})$ について von Bertalanffy モデルを使用した。

$$\hat{l}_{s,b}(t_{s,b,a,i}) = l_{\infty(s,b)}(1 - \exp(-K_{s,b}(t_{s,b,a,i} - t_{0(s,b)}))) \qquad (3.3)$$

ここで $l_{\infty(s,b)}$, $K_{s,b}$, $t_{0(s,b)}$ は，それぞれ極限体長（mm），成長係数（1／年），尾叉長が0となる年齢（年）を示す。

性別不明個体の尾叉長の理論値 $\hat{l}_{u,b}(t_{u,b,a,i})$ は，$\hat{l}_{m,b}(t_{u,b,a,i})$ と $\hat{l}_{f,b}(t_{u,b,a,i})$ に雌雄それぞれの割合を掛けた加重平均に等しいと仮定した。

$$\hat{l}_{u,b}(t_{u,b,a,i}) = \lambda \hat{l}_{m,a}(t_{u,b,a,i}) + (1-\lambda)\hat{l}_{f,a}(t_{u,b,a,i}) \qquad (3.4)$$

ここで λ（$0<\lambda<1$）は，標本から求めた雄の割合である。尤度関数（Kimura, 1980）は，

$$L = \prod_s \prod_b \prod_a \prod_i \frac{1}{\sqrt{2\pi}\sigma_{s,b}} \exp\left\{ -\frac{(l_{s,b,a,i} - \hat{l}_{s,b}(t_{s,b,a,i}))^2}{2\sigma^2_{s,b}} \right\} \qquad (3.5)$$

である。

Group 1〜3のデータを使用し，年齢－尾叉長の von Bertalanffy 成長式を推定した。成長式のパラメータは，地区や雌雄による成長差の有無について，可能な限り考慮した。l_∞ は地区，雌雄について考慮したが，K は地区によって小型魚の標本数が十分でないため，地区によらず一定とし雌雄のみを考慮した。また，発生初期段階のサンプルがないことに加え，産卵期に仔魚が伊豆諸島北部海域で広範囲に分布することから，t_0 は地区，雌雄によらず一定と仮定した。von Bertalanffy 成長式のパラメータを地区と雌雄について考慮し，以下の4つのケースに分けて推定した。

Case 1（地区別，雌雄別）

$$l_{\infty(m,1)},\ l_{\infty(f,2)},\ l_{\infty(m,3)},\ l_{\infty(f,1)},\ l_{\infty(m,2)},\ l_{\infty(f,3)},$$
$$K_{m,1} = K_{m,2} = K_{m,3},\ K_{f,1} = K_{f,2} = K_{f,3},$$
$$t_{0(m,1)} = t_{0(m,2)} = t_{0(m,3)} = t_{0(f,1)} = t_{0(f,2)} = t_{0(f,3)},$$
$$\sigma^2_{m,1},\ \sigma^2_{m,2},\ \sigma^2_{m,3},\ \sigma^2_{f,1},\ \sigma^2_{f,2},\ \sigma^2_{f,3},\ \sigma^2_{u,1},\ \sigma^2_{u,2},\ \sigma^2_{u,3}.$$

Case 2（地区込み，雌雄別）

$$l_{\infty(m,1)} = l_{\infty(m,2)} = l_{\infty(m,3)},\ l_{\infty(f,1)} = l_{\infty(f,2)} = l_{\infty(f,3)},$$
$$K_{m,1} = K_{m,2} = K_{m,3},\ K_{f,1} = K_{f,2} = K_{f,3},$$
$$t_{0(m,1)} = t_{0(m,2)} = t_{0(m,3)} = t_{0(f,1)} = t_{0(f,2)} = t_{0(f,3)},$$
$$\sigma^2_{m,1} = \sigma^2_{m,2} = \sigma^2_{m,3},\ \sigma^2_{f,1} = \sigma^2_{f,2} = \sigma^2_{f,3},\ \sigma^2_{u,1} = \sigma^2_{u,2} = \sigma^2_{u,3}.$$

Case 3（地区別，雌雄込み）

$$l_{\infty(m,1)} = l_{\infty(f,1)},\ l_{\infty(m,2)} = l_{\infty(f,2)},\ l_{\infty(m,3)} = l_{\infty(f,3)},$$
$$K_{m,1} = K_{m,2} = K_{m,3} = K_{f,1} = K_{f,2} = K_{f,3},$$
$$t_{0(m,1)} = t_{0(m,2)} = t_{0(m,3)} = t_{0(f,1)} = t_{0(f,2)} = t_{0(f,3)},$$
$$\sigma^2_{m,1} = \sigma^2_{f,1} = \sigma^2_{u,1},\ \sigma^2_{m,2} = \sigma^2_{f,2} = \sigma^2_{u,2},\ \sigma^2_{m,3} = \sigma^2_{f,3} = \sigma^2_{u,3}.$$

Case 4（地区込み，雌雄込み）

$$l_{\infty(m,1)} = l_{\infty(m,2)} = l_{\infty(m,3)} = l_{\infty(f,1)} = l_{\infty(f,2)} = l_{\infty(f,3)},$$
$$K_{m,1} = K_{m,2} = K_{m,3} = K_{f,1} = K_{f,2} = K_{f,3},$$
$$t_{0(m,1)} = t_{0(m,2)} = t_{0(m,3)} = t_{0(f,1)} = t_{0(f,2)} = t_{0(f,3)},$$
$$\sigma^2_{m,1} = \sigma^2_{m,2} = \sigma^2_{m,3} = \sigma^2_{f,1} = \sigma^2_{f,2} = \sigma^2_{f,3} = \sigma^2_{u,1} = \sigma^2_{u,2} = \sigma^2_{u,3}.$$

定置網で捕獲されたものは，定置網導入試験（東京都水産試験場，1993）の結果より尾叉長120mm 以上については十分に漁獲される。また，寄網と建切網においても，追い込んだ魚群をすくい上げるとき使用する網の目合いが8〜12節とタカベの魚体に対して小さいため，漁獲対象サイズの標本に偏りはないと考えられる。しかし，刺網については選択性の影響で漁獲対象サイズのサンプルが偏っている可能性がある。そこで，年齢－尾叉長の成長式の推定には漁業で収集した標本のうち，定置網と寄網，建切網のものを使用した。

2．年齢形質の違いの検討

耳石と鱗それぞれの年齢－尾叉長データの違いが，成長式の推定に及ぼす影響を調べた。Group 1の耳石と鱗による年齢の査定値を使用し，極限体長，成長係数，分散を雌雄別に推定したときの von Bertalanffy 成長式のパラメータと満年齢における尾叉長を比較した。

3．尾叉長－体重のアロメトリー式

性別 s の v 番目の個体（v=1, …, V_s）の体重 $w_{s,v}$ (g) とおき，加法誤差構造と乗法誤差構造の尾叉長－体重関係を以下のモデルで表す。

$$w_{s,v} = \hat{w}_s(l_{s,v}) + \varepsilon_{s,v} \quad \text{（加法誤差構造）} (3.6)$$

$$w_{s,v} = \hat{w}_s(l_{s,v}) e^{\varepsilon_{s,v}} \quad \text{（乗法誤差構造）} (3.7)$$

ここで $\hat{w}_s(l_{s,v})$ は，尾叉長 $l_{s,v}$ における体重の理論値を示す。$\hat{w}_s(l_{s,v})$ についてアロメトリー式を使用した。

$$w_s(l_{s,v}) = \alpha_s l_{s,v}^{\beta_s} \quad (3.8)$$

ここで，$\varepsilon_{s,v}$ は，平均 0，分散 σ^2_s (g^2) の正規分布に従う誤差を示す。また，v 番目の性別不明個体の体重の理論値 $\hat{w}_u(l_{u,v})$ は，(3. 4) 式と同様に雌雄の体重の理論値の加重平均に等しいと仮定した。

$$\hat{w}_u(l_{u,v}) = \lambda \hat{w}_m(l_{u,v}) + (1-\lambda)\hat{w}_f(l_{u,v}) \quad (3.9)$$

加法誤差構造，乗法誤差構造における，それぞれの尤度関数は，

（加法誤差構造）

$$L = \prod_s \prod_v \frac{1}{\sqrt{2\pi}\sigma_{s,v}} \exp\left\{ -\frac{(w_{s,v} - \hat{w}_s(l_{s,v}))^2}{2\sigma^2_{s,v}} \right\} \quad (3.10)$$

（乗法誤差構造）

$$L = \prod_s \prod_v \frac{1}{w_{s,v}\sqrt{2\pi}\sigma_{s,v}} \exp \left\{ -\frac{(\log w_{s,v} - \log \hat{w}_s(l_{s,v}))^2}{2\sigma^2_{s,v}} \right\} \quad (3.11)$$

となる。

Group 1～ 4のデータを使用しアロメトリー式を推定した。地区によって小型魚の標本数が十分でないため地区間の差は考慮せず，性別を雌雄込みと雌雄別，誤差構造を加法誤差と乗法誤差について考慮した。性別と誤差構造の組み合わせで，合計 4 種類のモデルを推定した。

4．パラメータ推定とモデル選択

未知パラメータは，統計解析ソフト R (version 2.1.0)（R Development Core Team, 2005）を使用し最尤法で推定した。パラメータ推定値の標準誤差は observed Fisher 情報量の逆行列を使用して求めた (Seber, 1989)。また，乗法誤差構造のアロメトリー式において，α の標準誤差はデルタ法を用いて推定した（Seber, 1982)。von Bertalanffy 成長式，アロメトリー式において，複数の候補としたモデルから，最適なモデルを赤池情報量規準（以下，AIC）

$$AIC = -2LL + 2p \quad (3.12)$$

を使用し選択した（Akaike, 1973)。ここで LL と p は，それぞれ最大対数尤度とパラメータ数を示す。

5．年齢－体重の von Bertalanffy 成長式

年齢－体重の von Bertalanffy 成長式を年齢－尾叉長の von Bertalanffy 成長式とアロメトリー式のパラメータ推定値を使用して求めた。

$$w_{s,b}(t_{s,b,a,i}) = w_{\infty(s,b)}(1 - \exp(-K_s(t_{s,b,a,i} - t_0)))^{\beta_s} \quad (3.13)$$

ここで $w_{\infty\,(s,b)}$ は極限体重（g）で $l_{\infty\,(s,b)}$ のときの体重を示す。

成　熟

生殖腺重量と体重から生殖腺指数（Gonad Somatic Index，以下 GSI）を求めた（羽生，小栗，1991)。

$$\text{GSI} = \text{生殖腺重量(g)} \times 100 / \text{体重(g)} \quad (3.14)$$

漁獲対象となっている個体の雌雄別の GSI の月変化を Area 2-1，Area 2-2，Area 2-3について調べた。また，産卵期である10月の漁獲対象サイズ以下の個体について，尾叉長と GSI，成熟状態の関係を調べた。さらに，雌雄それぞれについて年齢別成熟率を求めた。ここで，成熟状態は目視で観察し，雄で精巣が乳白色で膨らんでいるものを，雌で卵巣内に卵が形成されているものをそれぞれ成熟と判断し，雌雄とも産卵時期以外と変化がないものを未成熟と判断した。

結　果

輪紋数の計測

1．耳石と鱗の輪紋数査定

Group 2の耳石の輪紋は485個体中482個体を計測することができた（可読率 =0.998)。鱗の輪紋数は11,467個体を査定し11,311個体計測することができた（可読率 =0.986)。輪紋を計測することができなかった標本は，採取した鱗がすべて再生鱗であったものと，胸鰭周辺の鱗がほとんど剥がれ落ちていたため，査定に適した鱗が 1 枚もなかったものである。生殖腺を観察した結果，雄，雌，不明の個体数は，それぞれ7,843,

Table 3.2. The frequency at each ring group from 1994 to 2003 by fishing gear, area and year.

	Area	Fishing gear	Ring group	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
(Scale)	2-1	Gill net	1	18	55	58	141	29	0	57	33	77	55
			2	36	71	39	103	54	15	104	128	184	106
			3	41	72	20	28	8	19	99	171	124	98
			4	21	81	15	26	1	16	23	77	105	52
			5	2	17	6	8	0	11	2	25	26	19
			6	0	1	1	1	0	7	1	6	11	4
			7	0	0	0	0	0	0	0	1	2	0
			unreadable	1	5	2	1	0	3	2	13	8	7
	2-1	Set net	1	43		18		0	49	45	94	14	54
			2	85		6		5	149	162	140	34	56
			3	80		16		12	59	104	98	43	29
			4	31		6		10	21	23	34	24	25
			5	8		2		4	9	12	3	0	12
			6	0		0		1	3	4	2	0	1
			7	0		0		0	0	0	0	0	0
			unreadable	3		6		1	8	2	4	0	7
	2-2	Seine	1		2			28	104	21	89		35
			2		13			42	240	69	178		133
			3		34			4	107	62	68		91
			4		15			0	16	18	22		27
			5		1			0	17	10	5		6
			6		0			0	6	2	6		2
			7		0			0	0	1	0		0
			unreadable		2			0	3	2	15		2
	2-2	Gill net	1	8	7		17	77	35	179	117	54	22
			2	22	28		37	103	111	232	218	64	52
			3	97	28		7	15	55	178	107	24	38
			4	46	14		10	3	36	76	34	4	24
			5	4	1		5	3	36	53	36	1	9
			6	0	0		2	0	10	23	9	3	4
			7	0	0		0	0	0	3	3	0	0
			unreadable	5	1		1	0	1	7	13	0	2
	2-3	Bulk net	1	15	9	41	104	29	17	121	58	65	36
			2	29	28	75	106	224	166	105	226	143	167
			3	69	82	82	27	28	99	40	42	82	73
			4	43	88	120	36	12	11	16	21	22	32
			5	7	21	44	18	7	6	14	7	4	6
			6	1	0	8	4	2	0	2	1	3	1
			7	0	0	0	0	0	0	0	0	0	0
			unreadable	4	0	5	2	1	5	3	0	2	4

	Ring group	Area 2-1 Gill net			Area2-1 Set net		Area 2-3 Bulk net
		2001	2002	2003	2001	2002	2003
(Otolith)	1	10	89	26	93	21	26
	2	42	138	41	64	21	153
	3	113	116	31	60	33	88
	4	102	115	28	22	13	41
	5	36	60	28	5	0	5
	6	9	14	8	1	0	4
	7	2	3	1	0	0	1
	8	0	0	1	0	0	0
	unreadable	2	2	2	0	2	1

Table 3.3. Relationship of the number of rings between otolith and scale.

Otolith	Scale							
	1	2	3	4	5	6	7	unreadable
1	166	90	6	2				1
2	33	320	89	9	3			4
3	8	109	228	91	2	1		2
4	6	37	133	118	16	3		7
5	2	5	37	48	31	4		9
6		1	2	13	9	9	2	
7			2		2	2	1	
8						1		
unreadable		4	4	1				

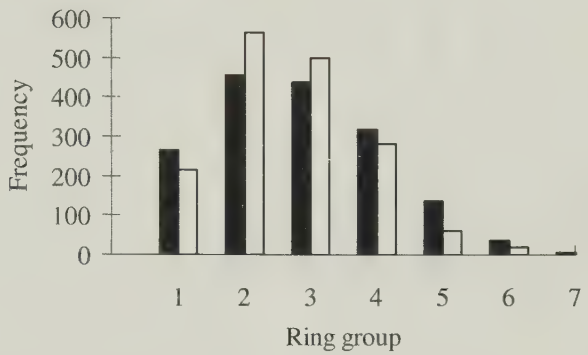

Fig. 3.2. The frequency of each ring group from counts of rings of otolith (black bars) and scale (white bars).

Table 3.4. The frequency of each ring group using otolith and scale for three age determinations.

Ring group	Otolith			Scale		
	1st	2nd	3rd	1st	2nd	3rd
1	26	23	26	36	26	31
2	153	154	152	167	163	158
3	88	84	88	73	89	97
4	41	44	40	32	30	25
5	5	8	7	6	8	8
6	4	3	4	1	1	0
7	1	2	1	0	0	0
unreadable	1	1	1	4	2	0

Table 3.5. Probability of observed value of number of rings in otolith (ϕ^{oto}) to mean number of rings in otolith (h'^{oto}).

ϕ^{oto}	h'^{oto}				
	1	2	3	4	5+
1	0.99	0.01	0.00	0.00	0.00
2	0.01	0.98	0.02	0.00	0.00
3	0.00	0.01	0.93	0.14	0.00
4	0.00	0.00	0.05	0.82	0.12
5+	0.00	0.00	0.00	0.05	0.88

7,375，71個体だった。大島定置網，大島刺網，寄網，建切網，大島以南刺網により漁獲された標本の耳石と鱗の年別の輪紋数組成を Table 3.2に示す。いずれの漁法による標本も輪紋数が1～3本の個体が多い。また，調査で捕獲した小型魚は，耳石，鱗ともに輪紋は形成されていなかった。これらの標本の年齢は第二章と同様に体長組成から0.5～1歳と判断した。

2．耳石と鱗の輪紋値の信頼性の評価

1,673個体の耳石と鱗の輪紋数の関係を比較したところ，耳石では1,664個体，鱗では1,650個体査定でき，共通に査定できたものが1,641個体であった。Table 3.3

Table 3.6. Probability of observed value of number of rings in scale (ϕ^{scl}) to mean number of rings in scale (h'^{scl}).

ϕ^{scl}	h^{scl}				
	1	2	3	4	5+
1	0.86	0.05	0.01	0.00	0.00
2	0.14	0.81	0.18	0.03	0.00
3	0.00	0.13	0.70	0.14	0.00
4	0.00	0.02	0.11	0.72	0.09
5+	0.00	0.00	0.00	0.11	0.91

Table 3.7. Point estimates, standard errors and Akaike Information Criterion (AIC) values of the each cases of the von Bertalanffy growth models.

Parameter		Point estimate	SE	Parameter		Point estimate	SE
Case 1				Case 2			
AIC : 55547.2				AIC : 56310.4			
$l_{\infty(m,1)}$	(mm)	185.6	0.404	$l_{\infty(m)}$	(mm)	191.0	0.263
$l_{\infty(m,2)}$	(mm)	191.7	0.412	$l_{\infty(f)}$	(mm)	195.0	0.263
$l_{\infty(m,3)}$	(mm)	193.1	0.302	K_m	(1/year)	1.58	0.0194
$l_{\infty(f,1)}$	(mm)	188.9	0.386	K_f	(1/year)	1.50	0.0169
$l_{\infty(f,2)}$	(mm)	195.7	0.406	t_0	(year)	0.290	0.00355
$l_{\infty(f,3)}$	(mm)	197.7	0.301	σ_m	(mm)	10.15	2.68
K_m	(1/year)	1.60	0.0195	σ_f	(mm)	11.26	3.17
K_f	(1/year)	1.51	0.0167	σ_u	(mm)	7.06	1.86
t_0	(year)	0.280	0.00362				
$\sigma_{m,1}$	(mm)	11.35	6.23	Case 3			
$\sigma_{m,2}$	(mm)	8.78	4.16	AIC : 55985.5			
$\sigma_{m,3}$	(mm)	10.00	3.77	$l_{\infty(1)}$	(mm)	187.3	0.281
$\sigma_{f,1}$	(mm)	11.25	5.93	$l_{\infty(2)}$	(mm)	193.7	0.295
$\sigma_{f,2}$	(mm)	9.32	4.39	$l_{\infty(3)}$	(mm)	195.4	0.218
$\sigma_{f,3}$	(mm)	12.15	5.38	K	(1/year)	1.55	0.0146
$\sigma_{u,1}$	(mm)	6.82	1.83	t_0	(year)	0.280	0.00365
$\sigma_{u,2}$	(mm)	15.25	147.11	σ_1	(mm)	9.67	2.39
$\sigma_{u,3}$	(mm)	8.50	8.24	σ_2	(mm)	9.10	3.05
				σ_3	(mm)	11.04	3.11
				Case 4			
				AIC : 56808.4			
				l_∞	(mm)	193.1	0.191
				K	(1/year)	1.54	0.0147
				t_0	(year)	0.290	0.00358
				σ	(mm)	10.14	1.67

に鱗の輪紋数に対する耳石の輪紋数の関係を示す。Fig. 3.1は耳石と鱗の輪紋の比較の写真である。耳石と鱗の輪紋数査定値の一致率は53%で，全体の半分しか一致しなかった。また，両者の輪紋数の出現頻度は2，3輪で鱗の査定数の方が多く，4輪以上で耳石の査定数の方が多かった。全体として耳石の輪紋数に対して，鱗の輪紋数が過小に査定される傾向があった(Fig. 3.2)。

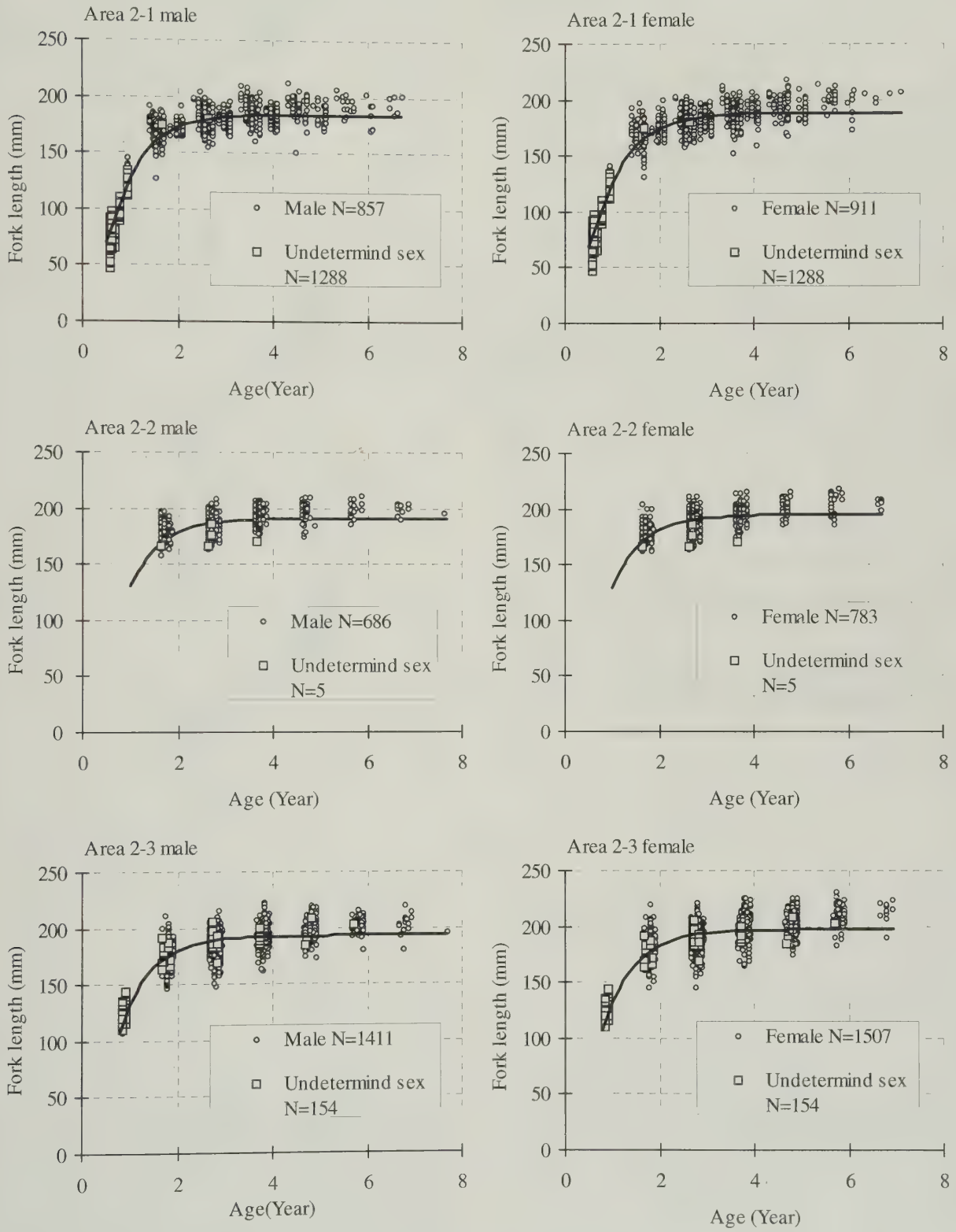

Fig. 3.3. Age-length data and the estimated von Bertalanffy growth curves of case 1.

Table 3.8. Comparison of estimated growth parameters and fork length at age of the von Bertalanffy growth model between counts of rings from otolith and scale by sex.

Parameter			Age	Otolith-male	Scale-male	Otolith-female	Scale-female
l_∞	(mm)	Estimate (SE)		185.8 (0.413)	185.9 (0.450)	190.8 (0.470)	190.0 (0.493)
K	(1/year)			1.23 (0.0299)	1.26 (0.0332)	1.20 (0.0285)	1.24 (0.0324)
t_0	(year)			0.09 (0.0184)	0.11 (0.0193)	0.09 (0.0184)	0.11 (0.0193)
		Fork length	1	125.7	125.5	127.4	127.0
		(mm)	2	168.8	168.2	171.9	171.6
			3	181.1	180.7	184.8	185.0
			4	184.5	184.3	188.5	189.1
			5	185.5	185.4	189.6	190.3
			6	185.8	185.7	189.9	190.7
			7	185.9	185.8	190.0	190.8

Table 3.9. Point estimates, standard errors and Akaike Information Criterion values (AIC) of the each cases of the allometric growth models.

Sex	Error structure	Parameter	Point estimate	SE
Separate	Multiplicative	AIC : 128406		
		$\ln(\alpha_m)$	-11.91	0.07133
		$\ln(\alpha_f)$	-12.70	0.06689
		α_m	0.00000670	0.00000048
		α_f	0.00000305	0.00000020
		β_m	3.191	0.01371
		β_f	3.348	0.01282
		σ_m	0.107	0.00019
		σ_f	0.112	0.00020
		σ_u	0.178	0.00095
Pooled	Multiplicative	AIC : 129834		
		$\ln(\alpha)$	-12.33	0.01938
		α	0.00000442	0.00000009
		β	3.275	0.00376
		σ	0.122	0.00016
Separate	Additive	AIC : 131477		
		α_m	0.00004126	0.000004146
		α_f	0.00001636	0.000001368
		β_m	2.844	0.0192
		β_f	3.028	0.0159
		σ_m	11.844	2.348
		σ_f	13.640	3.022
		σ_u	6.829	1.403
Pooled	Additive	AIC : 133411		
		α	0.00001934	0.000001214
		β	2.993	0.0120
		σ	12.44	1.682

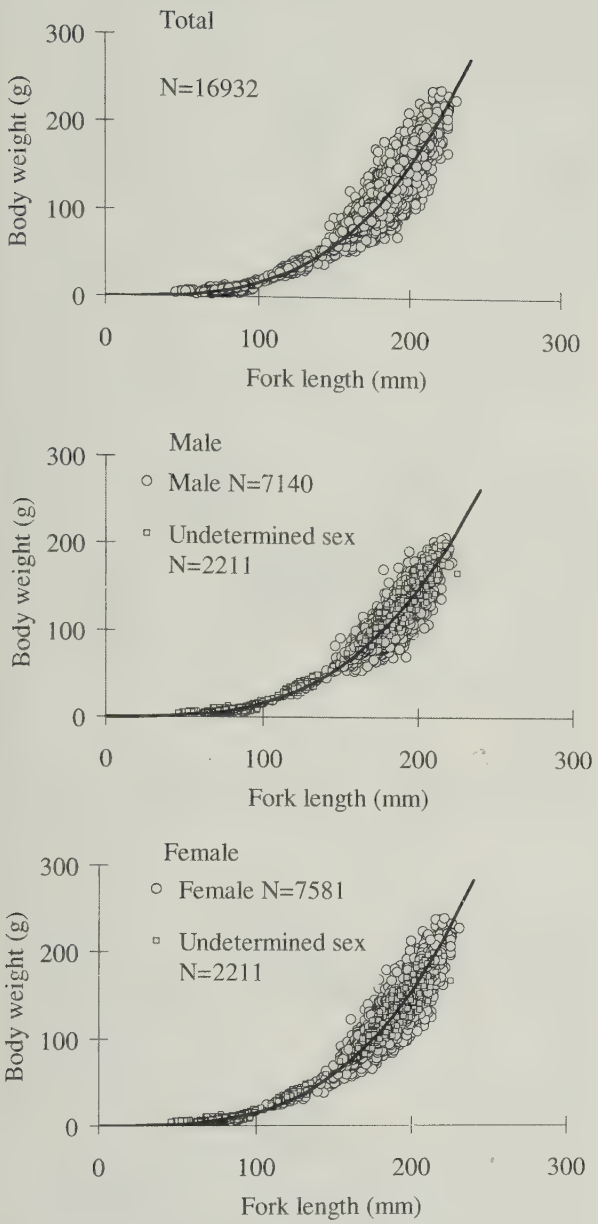

Fig. 3.4. Length-weight data and the estimated multiplicative error structure of the allometric growth model.

査定精度の検証に使用した標本のうち，耳石の輪紋数は319個体中318個体を査定することができた。輪紋が不明瞭なため，3回とも同一の1個体の輪紋数を査定することができなかった。また，鱗は1～3回目でそれぞれ315個体，317個体，319個体の輪紋を査定することができた。輪紋が不明瞭で計測できなかった個体は，1回目と2回目でそれぞれ4個体，2個体あり，そのうち1個体が同一であった。Table 3.4に耳石と鱗を3回ずつ査定したときの各回の輪紋数別出現個体数を示す。Table 3.5，3.6は耳石，鱗それぞれ h'^{oto}，h'^{scl} 本のとき多項分布モデルで推定した $p(\phi^{oto}|h'^{oto})$ と $p(\phi^{scl}|h'^{scl})$ の確率を示す。ここで，輪紋数が5本以上の個体数が少ないため，1つのグループ（5＋本）にまとめた。h と ϕ の一致率は，耳石の方が高く，読み取り誤差に関して耳石の精度が高いことを示す。

成長式の推定

Table 3.7は case 1～ case 4のパラメータ推定値とAIC の値を示す。AIC の値は Case 1のモデルが他のモデルと比較して小さかった。極限体長は大島，利島から式根島，神津島と伊豆諸島を南下するほど大きく推定された。また，すべての地区で極限体長は雌のほうが雄より約4 mm 大きかった。Fig. 3.3は Case 1の年齢－尾叉長関係の成長曲線を示す。タカベの成長は2歳まで急速に進む。Table 3.8に同一個体の耳石と鱗の査定値で推定した成長式のパラメータを示す。耳石と鱗それぞれのパラメータ推定値の標準偏差の範囲は，全て重なりあい，各年齢における尾叉長の推定値の差も1 mm 以下でほとんど同じであった。年齢形質の違いは成長式のパラメータの推定にほとんど影響していない。

Table 3.9に各モデルのパラメータ推定値とアロメトリー式の AIC の値を比較した結果を示す。AIC の値は，雌雄別，乗法誤差構造のモデルが最小であった。Fig. 3.4は乗法誤差構造の雌雄込みと雌雄別の尾叉長－体重のアロメトリー式を示す。

Table 3.10は Case 1から Case 4の年齢－尾叉長の von Bertalanffy 成長式と，性別の情報誤差構造のアロメトリー式のパラメータ推定値から求めた，年齢－体重関係の von Bertalanffy 成長式の地区別の満年齢における体重の理論値を示す。

成　熟

Fig. 3.5は漁獲対象サイズ以上の標本の，各月の雌雄別地区別の GSI の変化を示す。雌雄とも3～8月まで GSI は1.0以下で低い値であるが，9～12月にかけて増加し，10月にピークが見られた。10，11月に採集した満2歳以上の標本は，雄772個体，雌641個体で，そのうち GSI が産卵期以前と変わらない1.0以下のものは，雄3個体，雌2個体のみであった。このことから，満2歳以上では，雌雄ともほぼ全個体成熟していると考えられる。10月に大島で釣獲した満1歳の漁獲対象サイズ以下の標本147個体の生殖腺を調べた結果，雄，雌，不明の個体数はそれぞれ，73，61，13であった。Fig. 3.6に雌雄別の尾叉長階級ごとの GSI と成熟の有無のプロットを示す。成熟率は雄，雌でそれぞれ

Table 3.10. Estimated body weight of the each cases of the age-weight von Bertalanffy growth models.

	Case 1					
	Body weight (g)					
Age	Area 2-1		Area 2-2		Area 2-3	
	Male	Female	Male	Female	Male	Female
1	34.3	35.4	38.0	36.8	36.1	38.1
2	93.9	101.8	104.1	111.3	103.6	115.2
3	111.5	122.0	123.6	136.0	125.4	140.8
4	115.4	126.4	127.9	141.9	130.6	146.9
5	116.2	127.3	128.8	143.3	131.8	148.2
6	116.4	127.5	129.0	143.5	132.0	148.5
7	116.4	127.6	129.1	143.6	132.1	148.6

	Case 2		Case 3			Case 4
	Body weight (g)		Body weight (g)			Body weight(g)
Age	Male	Female	Area 2-1	Area 2-2	Area 2-3	
1	36.9	35.9	33.5	37.5	38.6	36.5
2	103.0	110.4	96.5	107.8	111.0	107.0
3	122.3	134.7	116.3	129.8	133.7	128.7
4	126.5	140.3	120.8	134.9	138.9	133.6
5	127.4	141.6	121.8	136.0	140.0	134.6
6	127.5	141.8	122.0	136.2	140.2	134.8
7	127.6	141.9	122.0	136.3	140.3	134.9

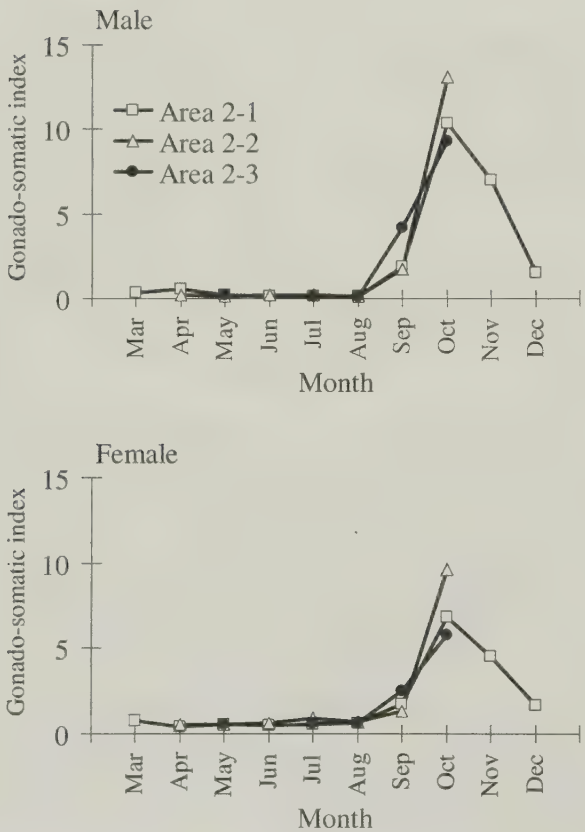

Fig. 3.5. Monthly changes of gonado-somatic index by area and sex.

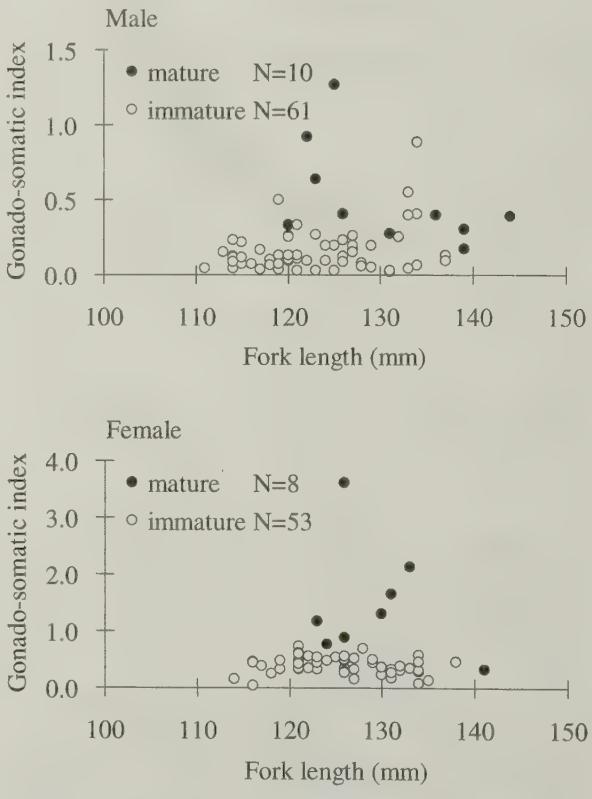

Fig. 3.6. Relationship between gonado-somatic index and fork length from survey samples in October. The black and open circles indicate mature and immature individuals, respectively.

Table 3.11. Estimated maturity at age by sex.

Age	Male			Female		
	Maturity	SE	Sample size	Maturity	SE	Sample size
1	0.14	0.0413	71	0.13	0.0432	61
2	0.99	0.0086	116	0.99	0.0077	129
3	1.00	—	122	1.00	—	134
4	1.00	—	147	1.00	—	141
5	1.00	—	90	1.00	—	114
6	1.00	—	38	1.00	—	39
7	1.00	—	10	1.00	—	7

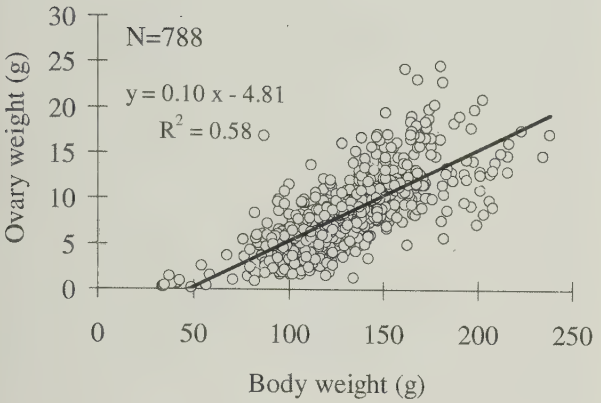

Fig. 3.7. Relationship between matured ovary weight and body weight. The open circles show the data.

14%，13%で，雌雄ともに尾叉長120mm以上の個体で成熟していた。Table 3.11に年齢別成熟率を示す。また，雌の体重と卵巣重量は比例関係にあった（Fig. 3.7）。

考　察

耳石と鱗それぞれについて，$p(\phi\ h)$ で h と ϕ の一致率は，鱗よりも耳石の方が高く，耳石の輪紋の査定精度が良いことが分かった。査定精度の評価基準としては，Beamish and Fournier (1981) や Chang (1982) など様々な基準が提案されている。これらについても，耳石と鱗の精度の比較を試みたが，いずれにおいても鱗より耳石の査定精度が高いことが示された。安藤ら (2004) は，2年半飼育した標本の耳石と鱗の輪紋を観察した結果，耳石の輪紋数は全て2本であったが，鱗で輪紋数は2本の個体の他に一部1本や3本の個体も出現していることを示している。天然の同一個体の鱗においても，飼育個体のように，鱗の輪紋数にバラツキが生じている可能性がある。鱗の輪紋数は複数の鱗から判断するため，同一個体での輪紋数のバラツキが，耳石より査定精度が劣る原因になると考えられる。

耳石と鱗の輪紋数が一致した個体は全体の半数であり，残りの半分は特に高齢部分で耳石の査定値に対して鱗の査定値が過小に推定される傾向があった。Beamish and McFarlane (1987) は，多くの魚種において，高齢になると成長が鈍化し，鱗の輪紋が形成されず，耳石や骨組織など他の年齢形質による査定と比較して過小推定になる傾向があることを指摘している。しかし，タカベの鱗の場合は，大型個体でも断切部と考えられる部位は形成れるものの，輪紋の間隔が非常に密に形成されているものが多かった。輪紋が密になることの読みにくさが原因となり，耳石と比較して鱗の輪紋数が過小に推定されると考えられる。本研究では1万個体以上の鱗の輪紋数を査定しており，査定方法，基準については習熟できていると考えるが，間隔が密な輪紋を判読することは非常に困難である。

Group 1の耳石と鱗による年齢査定結果を使用しvon Bertalanffy 成長式を推定したが，どちらのパラメータの点推定値もほとんど同じであった。第1輪形成前の小型魚の年齢は，尾叉長組成から十分査定が可能であり（Fig. 2.6），年齢形質の違いによる査定誤差が発生しない。また，高齢になると成長が非常に緩やかになるため，輪紋数の読み取り誤差があったとしても，年齢に対する尾叉長の関係がほとんど変化しない。これら二つの要因が重なり，鱗と耳石の違いによるvon Bertalanffy 成長モデルのパラメータの推定結果にほとんど差が生じなかったと考えられる。本研究における成長式の推定は，年齢と尾叉長，年齢と体重の関係を把握ことが目的である。このため，耳石と鱗の違いによる影響は小さい。

年齢－尾叉長関係の成長式として，加法誤差構造のvon Bertalanffy 成長モデルのみを推定したが，他の成長モデルや誤差構造も候補として考えることができる。成長モデルとしては，von Bertalanffy モデルの他に，Gompertz モデルや Logistic モデルなども候補となる。これらのモデルの当てはめも検討したが，von Bertalanffy モデルの方がAICの値が小さいうえ，データの範囲内では成長曲線にほとんど変化がなかった。また，年齢に従って分散が増加する乗法誤差や，年齢ごとに分散を分ける（Adachi *et al.*, 2000）など，

加法誤差以外の誤差構造についても検討したが，推定されるパラメータや成長曲線に大きな差はなかった．年齢に対する尾叉長の分散が年齢によらずあまり変化していないため（Fig. 3.4），加法誤差構造のみの考慮で十分と考えられる。

年齢－尾叉長関係の成長式とアロメトリー式の推定において，小型魚のサンプルが十分でなく，地区間の差の有無について考慮することが出来なかった。von Bertalanffy 成長モデルにおいては，アロメトリー式と同様の理由で成長係数を地区間で共通と仮定したが，生息海域の違いが成長係数の差として検出される可能性が考えられる。生後半年から1歳まで，小型魚の標本数は1,500個体以上で十分にある。しかし，その多くが Area 2-1で収集されたもので，Area 2-2で収集された標本はなかった。小型魚の標本収集に地区間の差があったため，地区ごとの成長係数に関する情報が十分に含まれていないと考えた。ここで，地区間で成長係数を共通と仮定したため，サンプル数の多い Area 2-1の個体の影響を受け，尾叉長の理論値に偏りが生じている可能性がある。そこで，予備的に小型魚の標本が十分にある Area 2-1と Area 2-3のデータを使用し，成長係数を地区別に推定し年齢ごとの尾叉長を比較した。成長係数は Area 2-3と比較し Area 2-1の方が3％大きく推定され，尾叉長の理論値の差は1歳で約1.7mm，2歳以降で0.5mm 以下であった。地区間の成長係数の考慮の有無によらず，年齢と尾叉長がほとんど変化しないことから，地区間の仮定の違いによる影響はわずかであると思われる。

満1歳で約15% の個体が成熟しており，漁獲対象となる前から一部個体が再生産に寄与していることがわかった。満1歳は尾叉長組成から十分に年齢を分離できるため，満2歳以上と混ざることはない。このため，年齢別成熟率の推定には，年齢査定誤差の影響を受けていない。有馬（1984）は，満1歳の小型魚における成熟割合の記述はないが，雄と雌でそれぞれ尾叉長130mm，120mm 以上の一部個体が成熟していることを示している。成熟サイズは本研究結果ともほぼ一致し，最小系が雌雄とも尾叉長120mm であると考えられる。性別は目視で生殖腺を観察したが，漁獲対象となる個体では性別不明個体の割合は0.3% と非常に小さく，この方法で十分性別判定が可能である。しかし，漁獲対象前の満1歳の個体では，不明個体の割合が15%，さらに満1歳未満の個体では，性別判定自体が非常に困難であった。小型魚の性別判定については，今後組織学的な方法の開発が必要である。

第四章　単位努力量あたり漁獲量の標準化

CPUE は，資源量に比例していると考えられ，相対的な資源の増減傾向の把握や，VAP におけるチューニングの指標として有用な情報である。しかし，その観測値には年による資源の変動以外の様々な要因を含んでいる。伊豆諸島北部海域においては，潮流や黒潮流路などの環境要因や，漁場の違いが操業に影響を与えることが指摘されている（有馬，1982；有馬，1995）。タカベの資源解析においても CPUE に含まれる年変動以外の要因を取り除き，資源量指数としての信頼性を高める必要がある。CPUE から年変動を抽出する方法は様々あり（庄野，2004；Maunder and Punt, 2004），一般化線形モデル（McCullagh and Nelder, 1989）が頻繁に用いられる。本章では，CPUE に対数正規誤差を仮定した Gavaris (1980) の方法をもとに，漁協から収集した水揚伝票と水温，黒潮の情報から，標準化を行った CPUE のうち年効果を抽出した。また，標準化したモデルに含まれる有意な効果について考察した。

試料と方法

試　料

伊豆大島周辺海域で操業する刺網，利島から式根島周辺海域で操業する寄網，神津島周辺海域で操業する建切網の水揚げ伝票をそれぞれ，伊豆大島漁業協同組合波浮事業所（旧波浮港漁業協同組合），にいじま漁業協同組合若郷事業所（旧若郷漁業協同組合），神津島漁業協同組合から1991～2003年の期間について収集し，操業ごとの水揚げ重量を調べた（1993年の寄網と建切網の水揚伝票は欠測）。また，各操業に対応する海洋環境の情報として，東京都水産試験場が伊豆諸島各島で観測している定地水温と一都三県漁海況速報，黒潮流型一覧表（千葉県水産研究センター，静岡県水産試験場，神奈川県水産総合研究所，東京都水産試験場，2004）を使用した。

移動に関する仮説

加入以降の資源の変動は，他の島や地区との間で移動がなければ，それぞれの島や地区ごとの変化としてとらえることができる。第三章の成長式の推定結果は，大島，利島から式根島，神津島の地区間で極限体長に差があることを示しており，伊豆諸島北部海域全体での大きな混ざり合いはないと考えられる。しかし，現在のところ加入以降どの程度，範囲で移動するか十分に解明されていない。本研究では，伊豆諸島北部海域

内の移動に関して，２つの仮説を考え解析を行った。伊豆諸島北部海域全体（Area 1）で小規模な混ざり合いがある場合を仮説１，島間の水深が深い箇所の間での移動は無く，地区内でのみ混ざり合っている仮定した場合を仮説２とした。仮説２において，地区の分割は基本的に島間で水深100m 以上あると移動しないと仮定し，第三章の場所と同じ範囲で，大島周辺海域（Area 2-1），利島から式根島周辺海域（Area 2-2），神津島周辺海域（Area 2-3）の３地区に分けた。ここで，Area 2-2は利島と鵜渡根島，鵜渡根島と新島の間も水深100m 以上あり，これらの島間でも地区を分離すべきであるが，新島若郷で水揚される寄網が新島，式根島周辺海域以外にも，利島，鵜渡根島周辺海域で操業しており，地区ごとの漁獲量や努力量が把握できないため１つの地区とした。

CPUE のモデルと効果

CPUE に含まれる年変動以外の要因を取り除くため，一般化線形モデルを使用し標準化を行った。CPUE に対数正規誤差を仮定し以下のモデルを考えた。

$$\log(\mathrm{CPUE})=\text{一般平均}+\text{主効果}+\text{交互作用}+\text{誤差} \quad (4.1)$$

ここで一般平均は各主効果の基準値における CPUE の理論値を示す。誤差は，平均０，分散σ^2の正規分布に従う。主効果には，水揚伝票から直接得られる情報として「年（Year）」,「月（Month）」,「場所（Point）」,「島漁法（Island, Fish）」と，海洋環境の情報として「水温（Tmep）」,「黒潮遠近（Kuro_1）」,「黒潮の型（Kuro_2）」の計７種類のうち各地区において利用可能なものを使用した。また，交互作用は二次の作用を使用した。

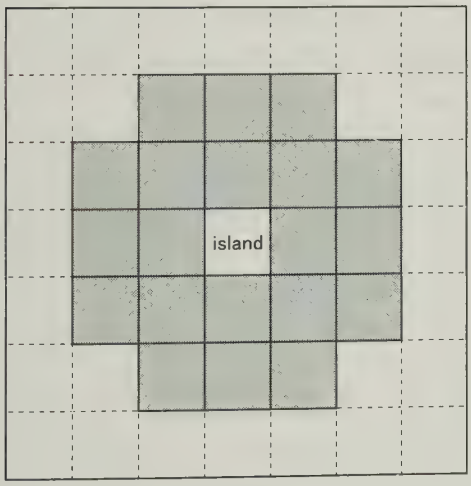

Fig. 4.1. Definition of the approach of the Kuroshio. When the Kuroshio was contained in gray frames of the forecasting of fishing and oceanographic condition of Tokyo, Kanagawa, Chiba and Shizuoka, it was judged that it approached. The frame is width of 10 minutes.

「年」と「月」の効果は，水揚伝票に記載されている日付から分類した。利島～新島の寄網の操業期間は５月下旬～10月上旬であるが，５月と10月の操業がいずれも数回ずつしかなかったため，それぞれ６月と９月の操業として扱った。同様に神津島の建切網でも，６月下旬と10月上旬の操業をそれぞれ７月と９月の操業として扱った。

神津島の建切網の水揚伝票には操業場所が記載されており，そこから神津島周辺，恩馳周辺と銭洲に分類し「場所」の効果とした。ここで，銭洲は本研究の対象地域外であるためデータから除外した。また，Area 1においては，大島の刺網，利島から式根島の寄網，神津島の建切網の違いを「島漁法」の効果とした。

黒潮流路は漁場に接近すると，タカベの群れが散らばることや，潮流が早くなり漁業の効率に影響を及ぼすため，CPUE が低下すると考えられる。そこで Area 2-2と Area 2-3について黒潮流路が漁場に接近するか否かを「黒潮遠近」の効果とした。接近の有無は，一都三県漁海況速報の黒潮流路の情報から「接近している」,「接近していない」の２種類に分類した。同速報には緯度経度10分のマスが記載されており，漁場がある島を含むマスから Fig. 4.1の灰色の範囲に，黒潮流路が含まれているかを接近の判断基準とした。また，土，日，祝祭日等の同速報が発行されていない日の黒潮流路は，前後の日の流路の中間に位置すると仮定し接近しているか否かを判断した。しかし，黒潮流路が大島周辺海域に接近することがほとんどないため，同海域では黒潮流路の接近か否かを効果として使用しなかった。Area 1と Area 2-1の標準化には，黒潮の蛇行の有無による周辺海域の環境の違いを「黒潮の型」の効果と考え使用した。黒潮の型の情報は「関東近海のマサバについて」に記載されている黒潮流型一覧表を使用した。「黒潮の型」の効果は，黒潮流路が伊豆諸島付近を通過する N, B, D, W 型と，蛇行する C 型の２つに分類した。また，本研究期間中に黒潮の特徴的な流型の１つである A 型海況の期間は無かった。

大島と利島から式根島周辺海域について，東京都水産試験場が伊豆諸島でほぼ毎日計測している Area 2-1の波浮口（大島）と Area 2-2の若郷（新島），野伏（式

根島）の定地水温情報を使用し「水温」の効果とした。欠測日の水温は前後の日の平均とした。また，利島から式根島周辺海域の水温は，若郷（新島）と野伏（式根島）の平均水温をこの地区の水温とした。Area 2-3では，神津島周辺と恩馳周辺の操業海域の違いを効果としたが，恩馳周辺海域の定地水温情報がないため，水温の効果を使用できなかった。

各地区の FULL MODEL

伊豆諸島北部海域の移動の仮説1，2に従い，Area 1, 2-1, 2-2, 2-3の CPUE 標準化を行った。Full モデルを以下に示す。

Area 1（伊豆諸島北部海域）

$$\log(CPUE)=Intercept+Year+Month+Kuro\_2+Fish,Island+(Year*Fish,Island)+(Fish,Island*Kuro\_2)+Error \quad (4.2)$$

Area 2-1（大島・刺網）

$$\log(CPUE)=Intercept+Year+Month+Kuro\_2+Temp+(Year*Temp)+(Month*Kuro\_2)+(Month*Temp)+(Kuro\_2*Temp)+Error \quad (4.3)$$

Area 2-2（利島から式根島・寄網）

$$\log(CPUE)=Intercept+Year+Month+Kuro\_1+Temp+(Year*Kuro\_1)+(Year*Temp)+(Month*Kuro\_1)+(Month*Temp)+(Kuro\_1*Temp)+Error \quad (4.4)$$

Area 2-3（神津島・建切網）

$$\log(CPUE)=Intercept+Year+Month+Kuro\_1+Point+(Year*Month)+(Year*Point)+(Month*Kuro\_1)+(Month*Point)+(Kuro\_1*Point)+Error \quad (4.5)$$

年の主効果を含む全組み合わせのモデルについて，最尤法でパラメータを推定し，AIC の値を比較し最適なモデルを選択した。AIC の値が最小のモデルのから各主効果と年を含む交互作用について最小2乗平均（Least Squared MEAN 以下，LSMEAN）を計算し，他の要因を平均化した効果を抽出した（高橋ら，1989）。主効果と年を含む交互作用の LSMEAN とその標準誤差の計算は，東京海洋大学品川地区情報処理センターに設置されている研究用計算機のアプリケーション SAS（version 8.02）を使用した。

ゼロキャッチの対応

建切網と寄網では，タカベとイサキが主漁獲対象で漁獲量全体に占める割合は，2003年の建切網でタカベ82%，イサキ11%，寄網でタカベ46%，イサキ51%であった。各回の操業の水揚げされた魚種別の重量を調べると，タカベを漁獲していないケースや，漁獲が数十キロと非常に少なくイサキを大量に漁獲しているケースがあった。本研究で使用する CPUE に対数正規誤差を仮定するモデルでは，タカベの漁獲が0の場合（ゼロキャッチ），Log（CPUE= 0）= −∞となってしまい，そのまま取り扱うことが出来ない。そこで，タカベとイサキの漁獲量に対して，タカベの漁獲量の割合が10%以下のものは，イサキのみを主漁獲対象とし，タカベは混獲されたものと考え，標準化のデータには使用しなかった。

結　果

Table 4.1は，仮説1に従い伊豆諸島北部海域で大島刺網，寄網，建切網の CPUE を標準化したモデルの全組み合わせの AIC の値を示す。AIC の値が最小だったのは年，島，黒潮の型の主効果と，年：島漁法，島漁法：黒潮の型の交互作用を含むモデルであった。Table 4.2は，仮説2に従い，各地区について標準化したモデルの全組み合わせの AIC の値を示す。AIC の値が最小であったのはそれぞれ，Area 2-1では年，水温，黒潮の型の主効果と年：水温の交互作用を含むモデル，Area 2-2では年，水温，黒潮遠近の主効果と水温：黒潮遠近の交互作用を含むモデル，Area 2-3では年，月，黒潮遠近，場所の主効果と月：場所の交互作用を含むモデルであった。

Table 4.3, 4.4は，仮説1と仮説2のそれぞれの地区における AIC の値が，最小のモデルのパラメータ推定値と主効果および年を含む交互作用の LSMEAN を示す。黒潮の型の効果は Area 1, 2-1とも伊豆諸島付近を通過する N, B, D, W 型の方が，蛇行する C 型より CPUE が高かった。黒潮遠近の効果について Area 2-3では，黒潮が接近すると CPUE が低くなることが示されたが，Area 2-2では黒潮が接近すると CPUE が高く，両地区で逆の傾向が見られた。Table 4.5, 4.6

は，仮説1と仮説2のそれぞれの地区における分散分析の結果を示す。

仮説1における各漁法のCPUE対数値の観測値と，標準化した年：島漁法の交互作用のLSMEANの年変動をFig. 4.2に示す。Fig. 4.3は年効果と，年：島漁法の交互作用における各年のLSMEANの点推定値と95%信頼区間である。信頼区間の幅は年，島漁法によらずほぼ一定であった。各地区のCPUEの年変動は，同様の傾向を示す箇所があるものの必ずしも一致していない。仮説2におけるCPUE対数値の観測値と，標準化した年効果のLSMEANをFig. 4.4に示す。LSMEANの95%信頼区間の幅は，Area 2-2の寄網とArea 2-3の建切網で年による差はあまり無いが，Area 2-1の刺網で他と比較し年変動が大きかった(Fig. 4.5)。

Fig. 4.6, 4.7は，仮説1と仮説2のそれぞれの地区におけるAICの値が最小のモデルの，CPUE対数値の理論値に対する標準化残差プロットを示す。また，Fig. 4.8, 4.9は，仮説1と仮説2のそれぞれの地区における年に対する標準化残差プロットを示す。いずれの仮説，地区においても，残差にシステマティックな傾向はみられなかった。

考　察

伊豆諸島北部海域全体のCPUEの変動は，年による増減があるものの増加，減少傾向は見られない。1991～2003年にかけて，同海域のタカベの資源水準は横ばいで推移している。各地区の変動は，1998年にCPUEが高くなり，その翌年に落ち込む共通の動向は見られるものの，各地区のCPUEの変動傾向は必ずしも一致していない。

場所による資源変動の違いの有無について，Area 1の年：島漁法の交互作用やArea 2-3の場所の主効果から検討することができる。Area 1の島漁法の効果は島，漁法の両者の違いが関わる複合的な要因であり，本研究で収集した情報からは別々に推定することができない。しかし，この中で年：島漁法の交互作用に注目すると，近年各漁法の操業形態や，使用する漁具に大きな変化がないことから，漁法の影響は小さいと考えられる。それぞれの島で独自の資源変動があり，地区間で大きな交流がない可能性がある。Area 2-3では，場所の主効果が選択されており，神津島と恩馳の間でCPUEに差があることが示された。しかし，年と場所の交互作用が有意でないことから，両地域間で異なる資源変動はなく，加入以降に交流があるものと考えられる。

Area 2-1, 2-2, 2-3では，AICの値のみで最適なモデルを一意に選択することができなかった。モデル間のAICの差が2未満場合，両者に有意な差はなく複数のモデルが候補となる（坂本ら，1983)。Area 2-1と2-3では，AICの値が最小のモデルのパラメータ数が最も少なかったものの，Area 2-2では，AICの値が2番目に小さい黒潮の効果を含まないモデルのパラメータ数の方が少なかった（Table 4.2)。黒潮が接近するか否かの効果（Kuro_1）に関して，Area 2-3は黒潮が漁場に接近するとCPUEが低下し，離れるとCPUEが増加するという，当初予想した通りの関係があった。しかし，Area 2-2では黒潮が漁場に接近するとCPUEが増加し，Area 2-3と逆の関係だった。Area 2-2は漁場の範囲がArea 2-3より広く(Fig. 1.1)，

Table 4.1. Akaike Information Criterion（AIC）values for each of the models in area 1.

Year	Month	Island,Fish	Kuro_2	Year*Island,Fish	Island,Fish*Kuro_2	AIC
○		○	○	○	○	3523.8
○	○	○	○	○	○	3526.8
○		○		○		3536.1
○		○	○	○		3538.1
○	○	○		○		3541.4
○	○	○	○	○		3543.4
○		○	○		○	3609.8
○		○				3610.8
○		○	○			3612.0
○	○	○	○		○	3615.1
○	○	○				3615.5
○	○	○	○			3617.0
○	○					4619.3
○	○		○			4619.8
○			○			4721.3

Table 4.2. Akaike Information Criterion (AIC) values of each of the models in area 2-1, 2-2, and 2-3.

(Area 2-1)

Year	Month	Kuro_2	Temp	Year*Temp	Month*Kuro_2	Month*Temp	Temp*Kuro_2	AIC
○		○	○	○				733.2
○	○			○				734.0
			○	○			○	735.2
○	○		○	○			○	735.5
○			○	○				735.8
○	○		○	○				736.1
○	○	○	○	○		○		736.8
○		○						737.2
○	○		○	○		○		737.9
○	○	○	○	○		○	○	738.6
○		○	○					739.2
○	○	○	○	○	○		○	739.3
○		○	○				○	739.4
○	○	○	○	○	○			739.8
○	○	○	○					741.2
○	○	○			○			741.6
○	○	○	○				○	742.2
○	○	○	○		○			742.8
○	○	○	○	○	○	○		744.0
○	○	○	○		○		○	744.3
○	○	○	○	○	○	○	○	744.8
○	○	○	○			○		746.0
○	○	○	○			○	○	746.8
○			○					748.0
○	○	○	○		○	○		748.7
○	○	○						750.3
○	○							750.3
○	○	○	○		○	○	○	750.6
○	○		○					751.8
○	○		○			○		755.2

Table 4.2. (*Continued*) (Area 2-2)

Year	Month	Temp	Kuro_1	Year*Temp	Year*Kuro_1	Month*Temp	Month*Kuro_1	Kuro_1*Temp	AIC
○		○	○					○	1350.8
○		○							1351.4
○	○	○				○			1352.1
○		○	○						1353.3
○	○	○	○			○			1354.0
○			○						1354.7
○	○	○	○			○		○	1355.4
○		○		○					1356.1
○	○								1357.8
○	○	○		○		○			1357.9
○		○	○	○					1358.0
○		○	○	○				○	1358.0
○	○	○	○					○	1358.5
○	○	○							1358.6
○	○		○						1359.4
○	○	○	○			○	○		1359.8
○	○	○	○	○		○			1359.8
○	○	○	○						1360.6
○	○	○	○			○	○	○	1361.2
○	○	○		○					1361.6
○	○	○	○	○		○		○	1361.8
○		○	○		○			○	1362.7
○	○	○	○	○					1363.6
○	○	○	○	○				○	1364.2
○	○		○				○		1364.8
○	○	○	○				○		1365.9
○		○	○		○				1366.1
○	○	○	○				○	○	1366.9
○	○	○	○		○			○	1367.3
○	○	○	○	○		○	○		1367.4
○	○	○	○		○	○			1367.5
○	○	○	○		○	○		○	1367.5
○			○		○				1367.7
○		○	○	○	○				1368.5
○		○	○	○	○			○	1368.8
○	○	○	○	○		○	○	○	1369.3
○	○		○		○				1369.5
○	○	○	○	○			○		1371.0
○	○	○	○		○				1371.3
○	○	○	○	○	○	○			1371.7
○	○	○	○	○			○	○	1372.6
○	○	○	○	○	○			○	1372.7
○	○	○	○	○	○				1372.9
○	○	○	○	○	○	○		○	1373.2
○	○	○	○		○	○	○	○	1373.5
○	○	○	○		○	○	○		1373.8
○	○		○		○		○		1375.2
○	○	○	○		○		○	○	1375.6
○	○	○	○		○		○		1377.0
○	○	○	○	○	○	○	○		1379.4
○	○	○	○	○	○	○	○	○	1379.9
○	○	○	○	○	○		○	○	1380.6
○	○	○	○	○	○		○		1380.7

Table 4.2. (*Continued*) (Area 2-3)

Year	Month	Point	Kuro_1	Year*Month	Year*Point	Month*Point	Month*Kuro_1	Point*Kuro_1	AIC
○	○	○	○			○			1457.2
		○	○		○	○			1457.2
		○	○			○		○	1458.2
		○			○	○			1458.9
○		○	○		○	○		○	1458.9
	○	○				○			1459.3
○	○	○	○			○	○		1460.6
○	○	○	○		○	○	○		1460.8
○	○	○	○			○	○	○	1461.7
○	○	○	○		○	○	○	○	1462.5
○		○	○						1465.3
○		○	○		○				1465.5
○		○	○					○	1466.4
○		○							1466.8
○		○			○				1466.9
○		○	○		○			○	1467.2
○	○	○	○						1468.4
○	○	○	○		○				1468.9
○	○	○	○					○	1469.7
○	○	○							1470.0
○	○	○			○				1470.4
○	○	○	○		○			○	1470.7
○	○	○	○	○		○			1471.5
○	○	○	○				○		1471.5
○	○	○		○		○			1471.8
○	○	○	○	○	○	○			1472.3
○	○	○	○	○		○		○	1472.4
○	○	○	○		○		○		1472.6
○	○	○	○				○	○	1472.9
○	○	○	○	○	○	○		○	1473.3
○	○	○		○	○	○			1473.5
○	○	○	○		○		○	○	1474.4
○	○	○	○	○		○	○		1474.6
○	○	○	○	○	○	○	○		1475.1
○	○	○	○	○		○	○	○	1475.2
○	○	○	○	○	○	○	○	○	1475.8
○	○	○		○					1483.3
○	○	○	○	○					1483.4
○	○	○	○	○				○	1484.7
○	○	○	○	○			○		1484.9
○	○	○	○	○	○				1485.1
○	○	○		○	○				1486.0
○	○	○	○	○			○	○	1486.1
○	○	○	○	○	○			○	1486.3
○	○	○	○	○	○		○		1486.5
○	○	○	○	○	○		○	○	1487.5
○			○						1513.9
○	○		○						1517.8
○	○		○				○		1521.5
○	○								1524.9
○	○		○	○			○		1530.7
○	○		○	○					1531.1

黒潮が接近した場合でも，その影響の少ない漁場の選択により，黒潮接近の効果がうまく抜き出せていない可能性がある。Area 2-3では神津島周辺と沖合の恩馳周辺の近接した地域間でも場所の主効果が有意であることから，より範囲が広い Area 2-2においても，場所の違いを効果として検討する必要があると考えられる。寄網の操業場所の情報の蓄積は，今後の課題である。

本研究を行った1991～2003年の期間，黒潮流路は，非大蛇行期のみであった。しかし，1976～1979年，1987年，1990年に断続的に大蛇行の A 型の期間があり，漁獲量，CPUE ともに減少し，タカベ漁業に対して大きな影響を及ぼしたことが指摘されている（米澤ら，2006）。本研究の対象期間後の2004年夏から，黒潮流路は A 型海況になっており，今後の CPUE の解析では A 型海況を考慮する必要がある。黒潮が A 型の場合，流路が神津島周辺海域に接近するため，黒潮の接近の効果として CPUE に与える影響を抽出することは可能かもしれない。しかし，A 型海況の情報が特定の年にしか存在しないため，本研究で使用した一般化線形モデルで A 型独自の効果を分離することは困難である。CPUE と環境の関わりについては今後精査する必要がある。

漁獲量がゼロのデータの扱いは，一般化線形モデルを用いた CPUE の標準化において，大きな問題となる（庄野，2004）。本研究で用いたタカベの漁獲が少ない操業を単純に削除する方法は，実際に漁業者への目的魚種の聞き取りなどによらない。このため，データから除外した操業の中に，タカベを漁獲対象としていたが漁獲できなかったケースがある場合は，CPUE を過大に推定する危険がある。そこで，ゼロキャッチデータも含む全ての CPUE データを使用する方法についても複数検討した。CPUE の全データに一定量を足しこむ方法を試したところ，理論値に対する残差プロットがゼロキャッチの影響で歪な傾向を示した。また，Delta 型二段階法（Lo, 1992 ; Stefansson, 1996）についても検討したが，ゼロキャッチが無い年もあり，全ての年でゼロキャッチ率が推定できなかった。さらにゼロキャッチの問題を無くすため，CPUE ではなく漁獲に着目した Catch モデル（Reed, 1986）を使用した標準化も検討した。タカベの場合，漁獲量が重量でしか把握できないことと，尾数に変換しても 1 回の操業で数千から数万尾漁獲されることから，Catch モデルには馴染まないと考えられる。いずれの方法においても，ゼロキャッチを含んだ CPUE データを使用し，標準化を適切に行うことができなかった。

Table 4.3. Point estimates and least square means (LSMEAN) and these standard error of the standardized log CPUE of the selected model in area 1.

Intercept		Point estimate	SE		
		8.486	0.120		
Main effect		**Point estimate**	**SE**	**LSMEAN**	**SE**
Year	1991	-	-	7.884	0.082
	1992	0.779	0.177	8.218	0.075
	1994	0.875	0.172	8.140	0.069
	1995	0.687	0.178	7.989	0.078
	1996	0.584	0.181	8.073	0.075
	1997	0.359	0.174	8.251	0.077
	1998	1.022	0.152	8.619	0.061
	1999	0.517	0.175	8.116	0.082
	2000	0.060	0.169	8.056	0.076
	2001	0.926	0.155	8.353	0.071
	2002	0.652	0.172	8.243	0.087
	2003	0.745	0.184	8.085	0.077
Kuro_2	type C	-0.350	0.119	8.145	0.055
	type B,D,N,W	-	-	8.192	0.028
Island,Fish	Area 2-1,Gill net	-2.465	0.199	6.771	0.056
	Area 2-2,Seine	0.591	0.198	8.825	0.036
	Area 2-3,Bulk net	-	-	8.911	0.039
Error		0.552			

Table 4.3. (*Contitued*)

Two-way interactions		Point estimate	SE	LSMEAN	SE
Year*Island,Fish	1991*Area 2-1,Gill net	-	-	6.235	0.152
	1992*Area 2-1,Gill net	-0.590	0.293	6.424	0.163
	1994*Area 2-1,Gill net	-0.702	0.276	6.408	0.138
	1995*Area 2-1,Gill net	-0.492	0.301	6.430	0.179
	1996*Area 2-1,Gill net	-0.254	0.295	6.565	0.163
	1997*Area 2-1,Gill net	0.213	0.294	6.807	0.173
	1998*Area 2-1,Gill net	-0.022	0.253	7.235	0.125
	1999*Area 2-1,Gill net	0.097	0.306	6.849	0.187
	2000*Area 2-1,Gill net	0.893	0.260	7.187	0.135
	2001*Area 2-1,Gill net	0.101	0.261	7.262	0.147
	2002*Area 2-1,Gill net	0.184	0.314	7.070	0.203
	2003*Area 2-1,Gill net	-0.204	0.289	6.776	0.148
	1991*Area 2-2,Seine	-	-	9.108	0.155
	1992*Area 2-2,Seine	-0.748	0.264	9.139	0.105
	1994*Area 2-2,Seine	-1.158	0.264	8.825	0.111
	1995*Area 2-2,Seine	-1.255	0.259	8.539	0.096
	1996*Area 2-2,Seine	-0.930	0.265	8.761	0.100
	1997*Area 2-2,Seine	-0.190	0.256	9.277	0.097
	1998*Area 2-2,Seine	-0.841	0.239	9.289	0.093
	1999*Area 2-2,Seine	-0.955	0.267	8.670	0.115
	2000*Area 2-2,Seine	-0.556	0.259	8.612	0.127
	2001*Area 2-2,Seine	-1.473	0.244	8.560	0.114
	2002*Area 2-2,Seine	-1.063	0.271	8.696	0.128
	2003*Area 2-2,Seine	-1.430	0.278	8.423	0.128
	1991*Area 2-3,Bulk net	-	-	8.310	0.119
	1992*Area 2-3,Bulk net	-	-	9.090	0.114
	1994*Area 2-3,Bulk net	-	-	9.186	0.107
	1995*Area 2-3,Bulk net	-	-	8.997	0.116
	1996*Area 2-3,Bulk net	-	-	8.894	0.120
	1997*Area 2-3,Bulk net	-	-	8.670	0.119
	1998*Area 2-3,Bulk net	-	-	9.332	0.098
	1999*Area 2-3,Bulk net	-	-	8.827	0.111
	2000*Area 2-3,Bulk net	-	-	8.370	0.131
	2001*Area 2-3,Bulk net	-	-	9.236	0.105
	2002*Area 2-3,Bulk net	-	-	8.962	0.107
	2003*Area 2-3,Bulk net	-	-	9.056	0.124
Island,Fish*Kuro_2	Area 2-1,Gill net*type B,D,N,W	0.780	0.187		
	Area 2-2,Seine*type B,D,N,W	0.412	0.156		
	Area 2-3,Bulk net*type B,D,N,W	-	-		
	Area 2-1,Gill net*type C	-	-		
	Area 2-2,Seine*type C	-	-		
	Area 2-3,Bulk net*type C	-	-		

Table 4.4. Point estimates and least square means (LSMEAN) of the main effect and these standard error of the standardized log CPUE of the selected model in area 2-1, 2-2, and 2-3.

(Area 2-1)

Intercept		Point estimate	SE		
		5.973	1.429		
Main effect		**Point estimate**	**SE**	**LSMEAN**	**SE**
Year	1991	-2.667	1.991	6.029	0.152
	1992	-2.314	2.103	6.527	0.141
	1993	2.315	1.701	7.014	0.102
	1994	0.310	1.714	6.471	0.124
	1995	-1.784	2.393	6.353	0.173
	1996	0.005	1.845	6.637	0.140
	1997	4.780	2.504	6.635	0.184
	1998	3.203	1.760	7.328	0.114
	1999	0.440	1.974	7.000	0.219
	2000	4.773	1.912	7.224	0.120
	2001	-0.005	1.879	7.286	0.134
	2002	2.152	4.323	7.052	0.471
	2003	-	-	6.819	0.135
Kuro_2	type C	-0.278	0.135	6.659	0.104
	type B,D,N,W	-	-	6.937	0.065
Temp		0.046	0.064		
Two-way interactions		**Point estimate**	**SE**		
Year*Temp	1991*Temp	0.087	0.087		
	1992*Temp	0.094	0.096		
	1993*Temp	-0.098	0.077		
	1994*Temp	-0.031	0.077		
	1995*Temp	0.061	0.106		
	1996*Temp	-0.009	0.084		
	1997*Temp	-0.231	0.119		
	1998*Temp	-0.125	0.079		
	1999*Temp	-0.012	0.095		
	2000*Temp	-0.203	0.086		
	2001*Temp	0.022	0.087		
	2002*Temp	-0.089	0.220		
	2003*Temp	-	-		
Error	0.4153				

Table 4.4. (*Continued*)

(Area 2-2)

Intercept		Point estimate	SE		
		9.743	0.677		
Main effect		Point estimate	SE	LSMEAN	SE
Year	1991	-	-	9.168	0.154
	1992	0.062	0.177	9.230	0.093
	1994	-0.301	0.184	8.867	0.102
	1995	-0.537	0.178	8.630	0.097
	1996	-0.371	0.176	8.797	0.085
	1997	0.226	0.178	9.394	0.101
	1998	0.153	0.178	9.321	0.094
	1999	-0.406	0.188	8.762	0.111
	2000	-0.543	0.191	8.625	0.120
	2001	-0.568	0.184	8.600	0.110
	2002	-0.397	0.193	8.771	0.120
	2003	-0.678	0.196	8.490	0.120
Kuro_1	approach	-	-	8.931	0.071
	not approach	-1.600	0.757	8.845	0.038
Temp		-0.023	0.027		
Two-way interactions		Point estimate	SE		
Temp*Kuro_1	temp*approach	-	-		
	temp*not approach	0.066	0.031		
Error	0.5234				

Table 4.4. (*Continued*)

(Area 2-3)

Intercept	Point estimate	SE
	8.286	0.156

Main effect		Point estimate	SE	LSMEAN	SE
Year	1991	-	-	8.554	0.129
	1992	0.443	0.159	8.997	0.105
	1994	0.442	0.171	8.996	0.095
	1995	0.254	0.162	8.808	0.107
	1996	0.109	0.172	8.663	0.108
	1997	0.178	0.171	8.732	0.125
	1998	0.738	0.161	9.292	0.102
	1999	0.187	0.169	8.741	0.099
	2000	0.149	0.171	8.703	0.131
	2001	0.639	0.165	9.193	0.106
	2002	0.419	0.168	8.973	0.097
	2003	0.244	0.189	8.798	0.118
Month	Jul.	-	-	8.819	0.056
	Aug.	-0.162	0.099	8.932	0.052
	Sep.	-0.020	0.108	8.861	0.056
Kuro_1	approach	-	-	8.789	0.059
	not approach	0.163	0.082	8.953	0.044
Point	Kouzu	-	-	8.624	0.042
	Onbase	0.269	0.113	9.118	0.052

Two-way interactions		Point estimate	SE
Month*Point	Jul.*Kouzu	-	-
	Aug.*Kouzu	-	-
	Sep.*Kouzu	-	-
	Jul.*Onbase	-	-
	Aug.*Onbase	0.550	0.150
	Sep.*Onbase	0.122	0.158
Error	0.5776		

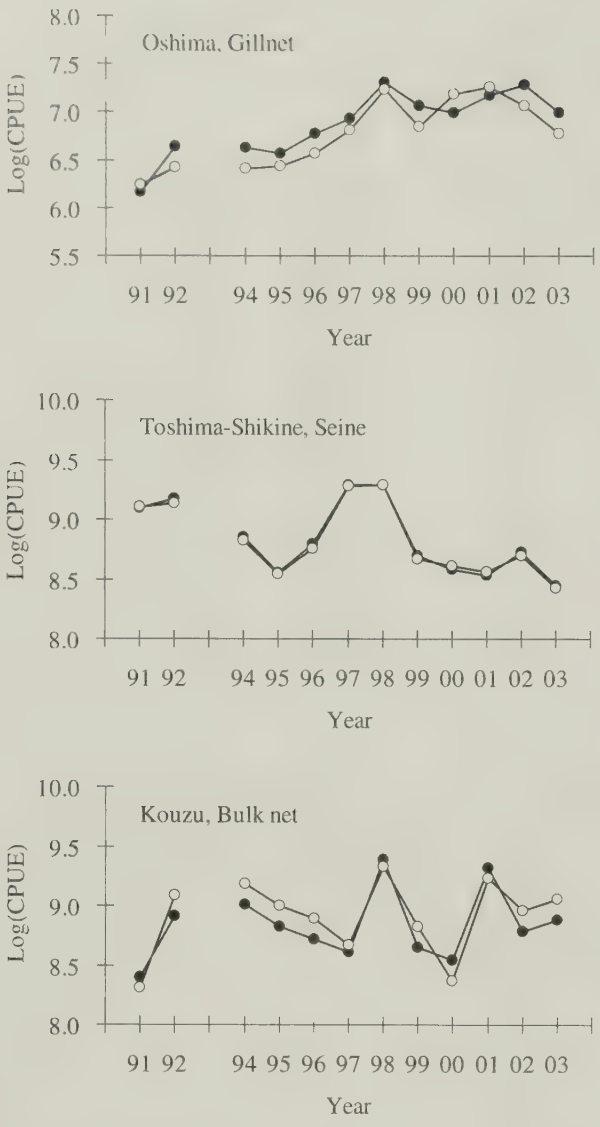

Fig. 4.2. Comparison of the least square means of the standardized log CPUE (open circles) and the nominal one (black ones) in area 1.

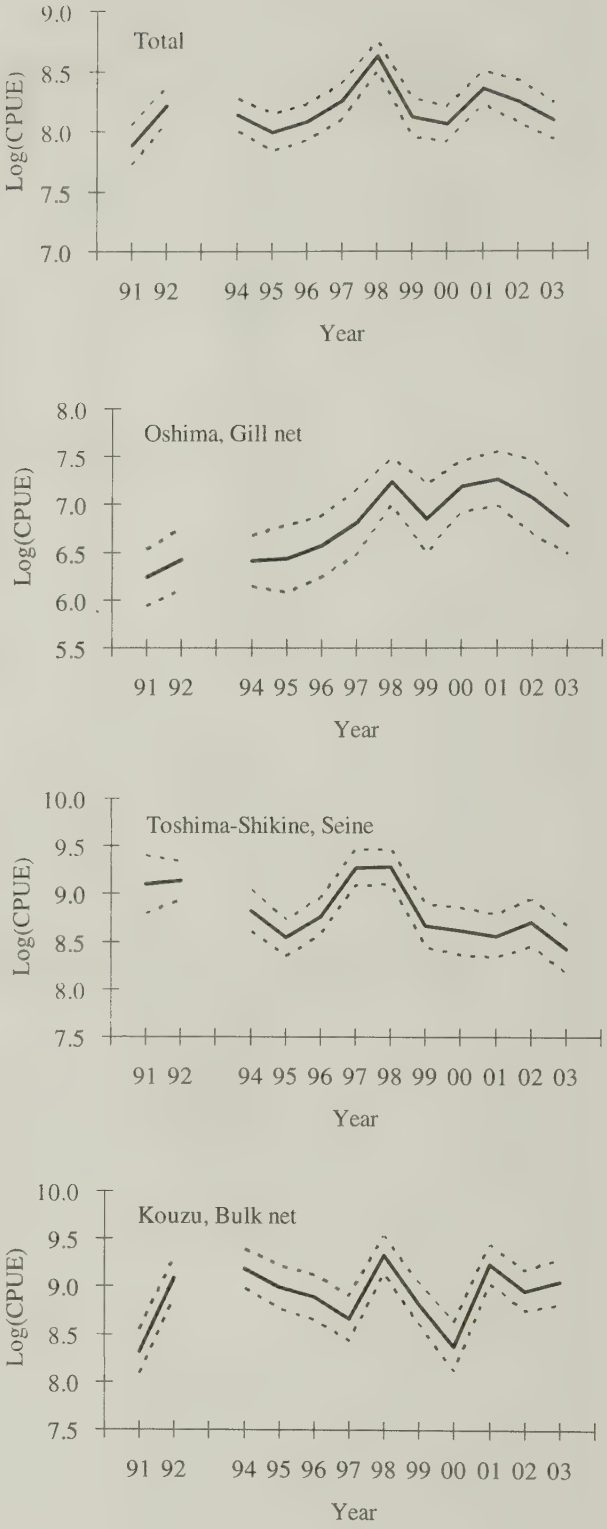

Fig. 4.3. Transition of the least square means of the standardized log CPUE in area 1. Solid and dotted lines indicate point estimates and its 95% confidence interval, respectively.

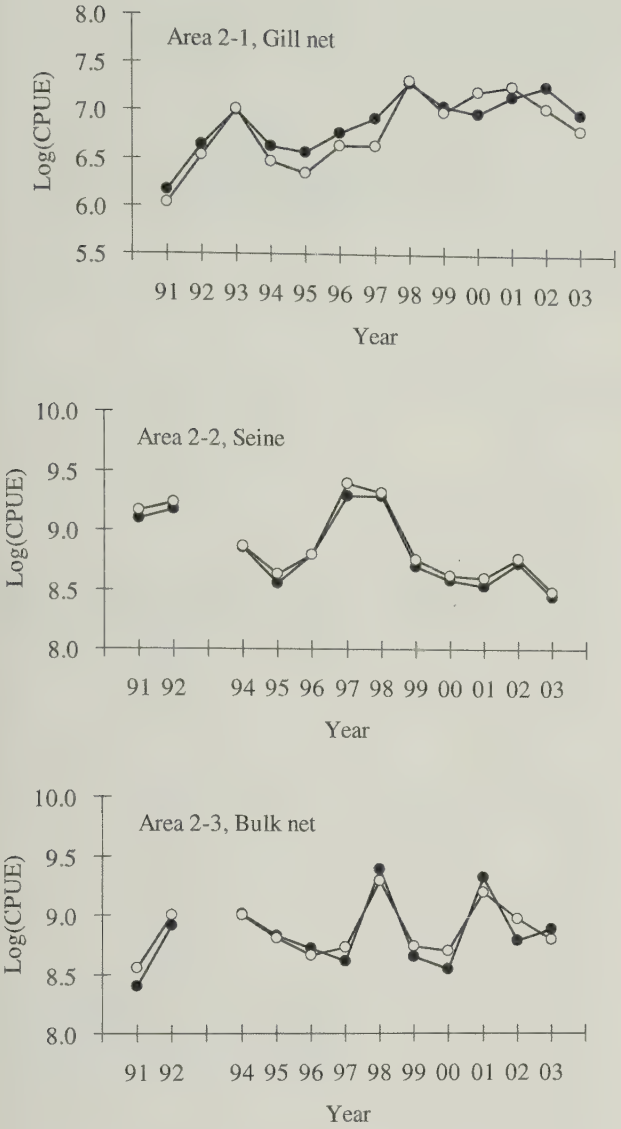

Fig. 4.4. Comparison of the least square means of the standardized log CPUE (open circle) and the nominal one (black circle) in area 2-1, 2-2, and 2-3.

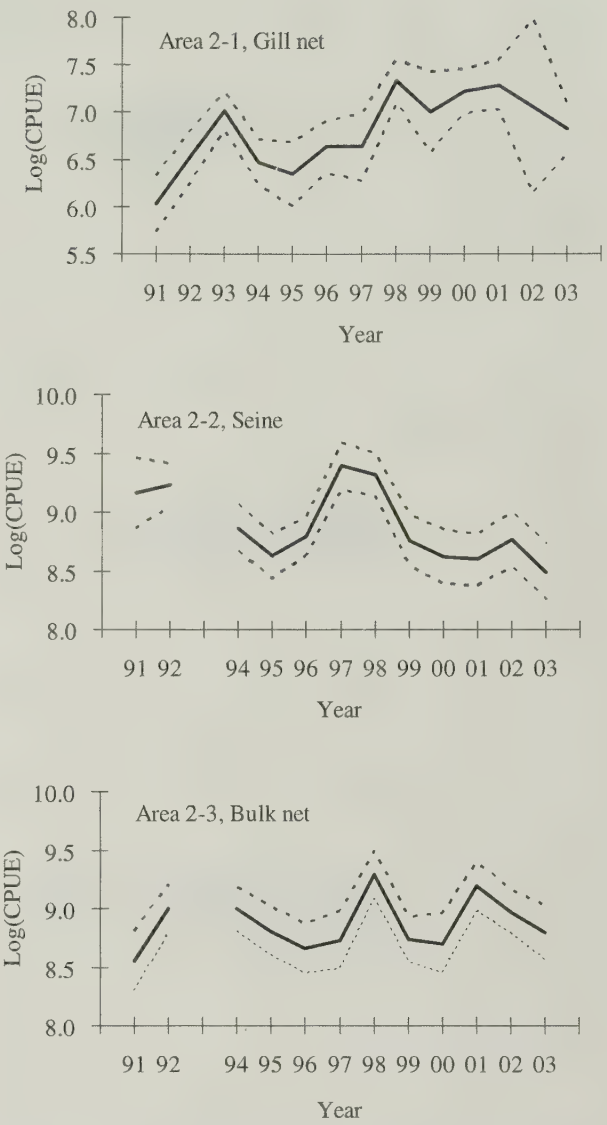

Fig. 4.5. Transition of the least square means of the standardized log CPUE in area 2-1, 2-2, and 2-3. Solid and dotted lines indicate point estimates and its 95% confidence interval, respectively.

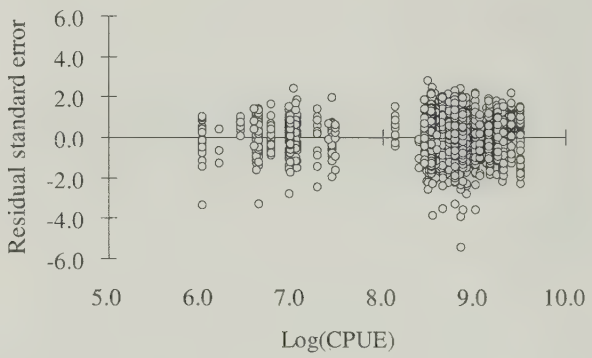

Fig. 4.6. Plot of the residual standard errors against the expected value of log CPUE in area 1.

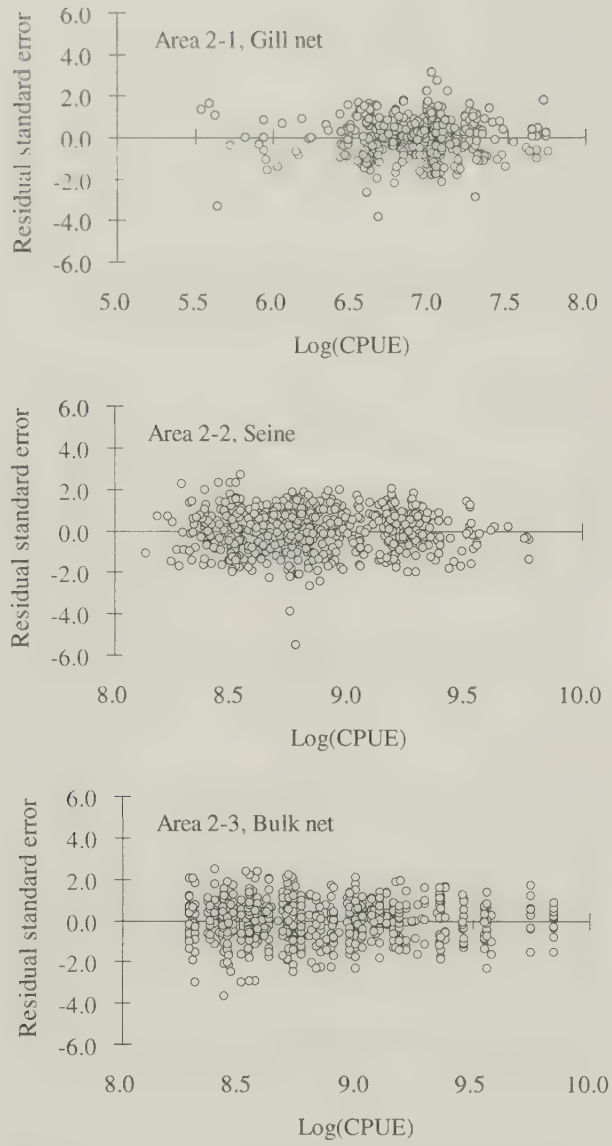

Fig. 4.7. Plot of the residual standard errors against the expected value of the log CPUE in area 2-1, 2-2, and 2-3.

Fig. 4.8. Plot of the residual standard errors against year in area 1.

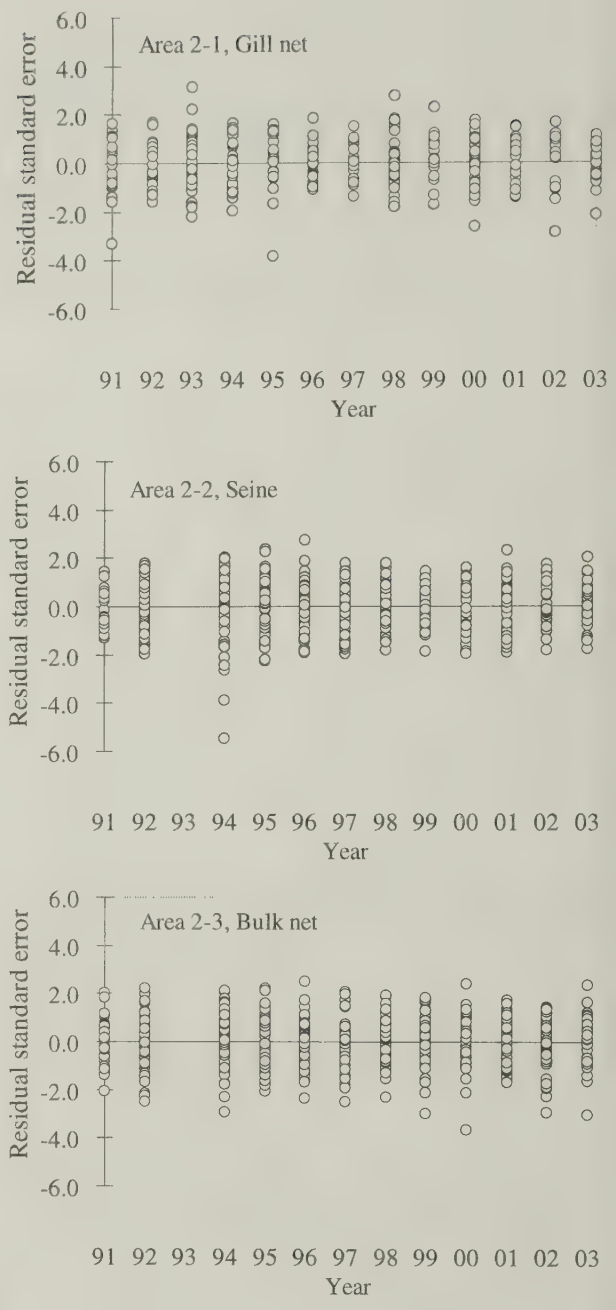

Fig. 4.9. Plot of the residual standard errors against year in area 2-1, 2-2, and 2-3.

Table 4.5. ANOVA results for the standardized log CPUE of the selected model in area 1.

Source	DF	Type III SS	Mean square	F value	Pr > F
Year	11	47.05	4.28	7.74	<.0001
Kuro_2	1	0.24	0.24	0.44	0.508
Island,Fish	2	617.56	308.78	558.99	<.0001
Year*Island,Fish	22	73.05	3.32	6.01	<.0001
Kuro_2*Island,Fish	2	9.90	4.95	8.96	0.0001

Table 4.6. ANOVA results for the standardized log CPUE in area 2-1, 2-2, and 2-3 of the selected model.

(Area 2-1)

Source	DF	Type III SS	Mean square	F value	Pr > F
Year	12	15.13	1.26	3.04	0.0005
Kuro_2	1	1.78	1.78	4.28	0.0394
Temp	1	0.02	0.02	0.04	0.8408
Year*Temp	12	12.01	1.00	2.41	0.0053

(Area 2-2)

Source	DF	Type III SS	Mean square	F value	Pr > F
Year	11	54.06	4.91	9.39	<.0001
Kuro_1	1	2.34	2.34	4.46	0.0351
Temp	1	0.21	0.21	0.4	0.5258
Kuro_1*Temp	1	2.29	2.29	4.37	0.0369

(Area 2-3)

Source	DF	Type III SS	Mean square	F value	Pr > F
Year	11	26.56	2.41	4.18	<.0001
Month	2	1.34	0.67	1.16	0.3136
Kuro_1	1	2.30	2.30	3.98	0.0466
Point	1	29.44	29.44	50.97	<.0001
Month*Area	2	8.66	4.33	7.49	0.0006

タカベを混獲されたと考える基準を5%，15%，20%に変化させたときの推定結果に与える影響について検討したが，選択される効果は同じで，推定されるCPUEの年トレンドもほぼ同じであった。このことから，タカベが主漁獲対象でないと考える基準の割合は，解析結果に大きな影響を与えないと考えた。

第五章　資源量推定

第三章で得られた輪紋数組成と，第四章で標準化したCPUE，そして漁獲量の情報があるとチューニングVPAで年別年齢別資源尾数を推定することができる。伊豆諸島周辺海域におけるタカベの資源量推定は，過去に数件VPAによるものが実施されている（東京都水産試験場大島分場，1995；東京都水産試験場，2000）。しかし，これらの研究は鱗による年齢組成を使用しているため，年別年齢別漁獲尾数が耳石を使用して推定した場合と比較し，若齢に偏っているものと考えられる。さらに，2000年以降は資源状態に関する報告がほとんどなされておらず，資源状況について十分な把握がなされていない。本章は，伊豆諸島北部海域において，資源量推定を行い，現状評価と資源管理に必要な情報を得ることを目的とする。CPUEの観測誤差と年齢の読み取り誤差，鱗と耳石の年齢形質の違いなどを考慮し，シミュレーションによりパラメータと資源量推定値に与える影響を調べた。また，YPR，SPR解析を行い，現在の漁獲圧とそれが変化させた場合の影響についても評価した。

試料と方法

試　料

年齢別漁獲尾数を推定するため，第三章で査定した耳石と鱗の輪紋数データを使用した。水揚伝票を伊豆

大島漁業協同組合，にいじま漁業協同組合と神津島漁業協同組合から収集し，各年の島別漁法別漁獲重量を調べた。水揚伝票上の記載により，三宅島や銭洲など伊豆諸島北部海域の本研究対象地域以外の場所での操業が確認できる場合は，それらをデータから除外した。また，水揚伝票を収集していない地区のタカベの漁獲重量は，東京都の漁獲統計資料「東京都の水産」の年別漁協別漁獲量を使用した。チューニングに使用するCPUEは，第四章で標準化したCPUEの年効果と，年と島漁法の交互作用のLSMEANを使用した。

年別年齢別漁獲尾数の推定

年別年齢別漁獲尾数の推定にあたりi番目の漁業（i=1, …, I），a歳（a=1, …, A），y年の標本数を$D_{i,a,y}$とすると，i番目の漁業のa歳，y年の年齢割合$\theta_{i,a,y}$は，

$$\theta_{i,a,y}=\frac{D_{i,a,y}}{\sum_{k=1}^{A}D_{i,k,y}} \tag{5.1}$$

となる。漁獲統計が暦年の集計値であるため，1月1日を起算日とし，輪紋数を年齢に変換した。第三章と安藤ら2004の飼育魚の知見から，耳石の方が真の年齢を当てる確率が高く，読み取り誤差が小さい。そこで，年別年齢別漁獲尾数を推定するさい，耳石の査定値が正しいと考え，鱗の年齢組成の偏りを耳石の基準に変換した。鱗で査定したi番目の漁業のa'歳，y年の標本数$D'_{i,a',y}$を，鱗の年齢に対する耳石の年齢査定値の出現割合を使用し，以下の式で変換した。

$$D_{i,a,y}=\sum_{a'=1}^{A}p(a\mid a')D'_{i,a',y} \tag{5.2}$$

ここで，$p(a|a')$は鱗の年齢がa'歳の時，耳石の年齢がa歳となる出現割合を示す。

i番目の漁業のa歳，y年の漁法別年別年齢別漁獲尾数$C_{i,a,y}$を，総漁獲重量$Y_{i,y}$と，1尾あたりの平均体重$\overline{W}_{i,y}$から，以下の式で求めた。

$$C_{i,a,y}=\theta_{i,a,y}Y_{i,y}/\overline{W}_{i,y} \tag{5.3}$$

Area 1で大島刺網，大島定置網，寄網，建切網，大島以南の刺網の5種類，Area 2-1で刺網と定置網の2種類，Area 2-2で寄網と刺網の2種類，Area 2-3で建切網と刺網の2種類の漁法別年別年齢別漁獲尾数を推定した。資源量推定は，Area 2-3で1994～2003年の10年間について行った。また，大島の定置網（Area 2-1）と寄網（Area 2-2）で1997年以前の年齢組成データが不十分であったため（Table 3.2），Area 1，Area 2-1，Area 2-2では，1998～2003年の6年間についてのみ資源量推定を行った。

2002年の寄網の年齢組成データは欠測しているが，寄網と建切網は漁法が類似しており，2001年と2003年の年齢組成を比較すると，いずれも，2輪の割合が最も高く，両者とも1輪，3輪，4輪，5輪以上の順で小さくなっている（Table 3.2）。よって，2002年の寄網の年齢組成は，同年の建切網の年齢組成と等しいと仮定し推定した。また，神津島の刺網漁業の年齢組成は，利島から式根島の刺網漁業のものを使用し，年別年齢別漁獲尾数を推定した。

資源量推定

a歳，y年における初期資源尾数と漁獲尾数は，以下の資源動態モデルで表せる。

$$N_{a,y}=N_{a-1,y-1}\exp\left\{-(F_{a-1,y-1}+M)\right\} \tag{5.4}$$

$$C_{a,y}=E_{a,y}N_{a,y} \tag{5.5}$$

$$E_{a,y}=\frac{F_{a,y}}{F_{a,y}+M}\left\{1-\exp(-F_{a,y}-M)\right\} \tag{5.6}$$

また，(5.4) 式と (5.5) 式から，

$$C_{a-1,y-1}-N_{a,y}E_{a-1,y-1}\exp(F_{a-1,y-1}+M)=0 \tag{5.7}$$

と，まとめることができる。ここで$E_{a,y}$，$F_{a,y}$は，それぞれa歳，y年における漁獲率と漁獲係数を示す。Mは自然死亡係数で加入以後，年，年齢によらず一定と仮定した。Mの推定は田内・田中の方法（田中，1960）を使用し，寿命を7歳と仮定しM=2.5÷7=0.357とした。$F_{a,y}$が与えられたとき，(5.7) 式における未知パラメータは$F_{a\text{-}1,y\text{-}1}$のみとなる。$F_{a\text{-}1,y\text{-}1}$の数値解は，ニュートン法を使用して推定した。タカベの漁獲物中の5歳以上の出現割合が少ないことから，これらをプラスグループとしてまとめた。また，高齢で成長が鈍化することから（Fig. 3.5），4歳と5＋歳で選択率に差はないと考え，$F_{4,y}=F_{5+,y}$と仮定し，プラスグループの資源尾数を以下の式で求めた（平松，2001）。

$$N_{5+,y}=N_{5+,y-1}\exp\left\{-(F_{5+,y-1}+M)\right\}+N_{4,y-1}\exp\left\{-(F_{4,y-1}+M)\right\} \tag{5.8}$$

最近年2003年の1～4歳のFは，$F_{4,2003}$をパラメータとし，最近年の各漁業の選択率が過去3年の選択率の平均であると仮定し推定した。

$$F_{a,2003}=\sum_{i=1}^{I}\left(\frac{\sum_{b=1}^{3}F_{i,a,2003-b}}{\sum_{b=1}^{3}F_{i,4,2003-b}}F_{i,4,2003}\right)$$

$$=\sum_{i=1}^{I}\left(\frac{\sum_{b=1}^{3}F_{i,a,2003-b}}{\sum_{b=1}^{3}F_{i,4,2003-b}}\frac{C_{i,4,2003}}{\sum_{j}C_{j,4,2003}}F_{4,2003}\right) \quad (5.9)$$

y年におけるi番目の漁法の対数変換したCPUEの観測値$\ln(u_{i,y})$は，平均0，分散σ^2の正規分布に従うと仮定した（田中，1999）。

$$\ln(u_{i,y})=\ln q_i\sum_{a}s_{i,a,y}\overline{N}_{a,y}+\varepsilon_{i,y} \quad (5.10)$$

$$\overline{N}_{a,y}=\frac{1}{F_{a,y}+M}N_{a,y}\left[1-\exp\{-(F+M)\}\right] \quad (5.11)$$

$$s_{i,a,y}=\frac{F_{i,a,y}}{\underset{a}{Max.}F_{i,a,y}} \quad (5.12)$$

$$F_{i,a,y}=\frac{C_{i,a,y}}{\sum_{j}C_{j,a,y}}F_{a,y} \quad (5.13)$$

$$\varepsilon_{i,y}\sim N(0,\sigma^2) \quad (5.14)$$

$s_{i,a,y}$，$u_{i,y}$，q_iはそれぞれ，i番目の漁業，a歳，y年における選択率，i番目の漁業，y年におけるCPUEの観測値，i番目の漁業における漁具能率を示す。未知パラメータはADAPT型VPAを使用し，最小2乗法でCPUEの理論値と実測値の残差が最小になる組み合わせのq_iと$F_{4,2003}$を推定した（Gavaris, 1988）。目的関数は，

$$\mathrm{RSS}=\sum_{i=1}^{I}\frac{1}{\omega_i}\sum_{y=1}^{Y}\left(\ln u_{i,y}-\ln q_i\sum_{a}s_{i,a,y}\overline{N}_{a,y}\right)^2 \quad (5.15)$$

である。ここでω_iはi番目の漁業の重み項で，iが2以上の場合，CPUE標準化で求めた島漁法の効果のLSMEANの分散を使用した。CPUEの実測値には，Area 1で建切網，寄網，刺網の3種類の年と島漁法の交互作用のLSMEANを，Area 2-1で刺網，Area 2-2で寄網，Area 2-3で建切網の年効果のLSMEANをそれぞれ使用した。最適解の探索はSimplex法（Nelder and Mead, 1965）を使用した。

誤差評価・感度解析

年別年齢別漁獲尾数とCPUEに含まれる誤差を考慮し，シミュレーションにより誤差評価を行った（Haddon, 2001）。年別年齢別漁獲尾数とCPUEの誤差を含んだリサンプリングデータを作成し，チューニングVPAを1,000回繰り返し，パラメータと資源量推定値の平均と標準誤差を求めた。年別年齢別漁獲尾数のリサンプリングデータは，第三章の輪紋数観測値ϕ本と真の輪紋数h本を年齢に置き換え，i番目の漁業のa歳，y年の標本数$\tilde{D}_{i,a,y}$を，多項乱数$\delta_{i,y,\phi,h}$を用いて作成した。標本数$\tilde{D}_{i,a,y}$は以下の式で求めた。

$$\tilde{D}_{i,a,y}=\sum_{h=1}^{H}\delta_{i,y,\phi=a,h} \quad (5.16)$$

ここで，$\delta_{i,y,\phi,h}$は$h=1,\cdots,A$について$n=D_{i,h,y}$，$p_1=p(\phi=1\ h)$，$p_2=p(\phi=2|h)$，$\cdots$，$p_5=p(\phi=5|h)$の多項分布から発生させた乱数である。耳石の査定誤差は$\phi=\phi^{oto}$，$h=h'^{oto}$，鱗の査定誤差は$\phi=\phi^{scl}$，$h=h'^{scl}$として乱数を発生させ，（5.16）式と（5.1）式，（5.3）式を使用し漁法別年別年齢別漁獲尾数に変換した。CPUE対数値のリサンプリングデータは，チューニングVPAで求めたCPUEの理論値に正規乱数を加え作成した。ここで，正規分布の分散はCPUEの残差から推定した（Efron and Tibshiram, 1993）。また，耳石と鱗それぞれの年齢査定の読み取り誤差に関して，両者の違いがパラメータと資源量推定値の変動係数に与える影響を評価した。

年別年齢別漁獲尾数を推定するさい，耳石に対する鱗の年齢査定値の偏りを考慮し，鱗の年齢組成を耳石の年齢組成に変換した。しかし，本研究以前では，鱗の年齢組成情報しかなかなく，耳石による年齢組成と比較して過小推定になっていると考えられる。そこで，耳石の年齢情報を使用した場合と，使用しない場合の年別年齢別漁獲尾数をArea 2-3（神津島）を例として作成し，資源量推定値とパラメータ推定値に与える影響を評価した。

感度解析として，各地区について，自然死亡係数の値を±10, 20%変化させたとき資源量推定値に与え

る影響を評価した。また，10年間の年齢別漁獲尾数データが使用できるArea 2-3についてレトロスペクティブ解析を行い最近年の推定値に偏りがあるかを調べた。

チューニングVPAによる資源量推定と誤差評価はMicrosoft® Excelのマクロ機能を使用しVisual Basic for Applications（VBA）のプログラムを作成し計算した。計算に使用したVBAプログラムをAppendix Aに示す。

資源の現状評価

資源の現状評価を行うため，加入あたり漁獲量（YPR）と加入あたり産卵親魚量（SPR）を各地区について求めた（松宮，1996）。SPRは加入1個体の生涯における期待産卵数である。生殖腺重量は親魚体重と比例関係にある（Fig. 3.8）。また，産卵数と生殖腺重量が比例関係にあると考え，期待産卵量は親魚体重に比例すると仮定した。YPRとSPRは，それぞれ，

$$YPR = \sum_{a=1}^{7} E_a S_a W_a \qquad (5.17)$$

$$SPR = \sum_{a=1}^{7} fr_a S_a W_a \qquad (5.18)$$

$$S_{a+1} = S_a \exp\{-(F_a + M)\} \quad (\text{ただし } S_1=1) \qquad (5.19)$$

$$E_a = \frac{F_a}{F_a + M}\{1 - \exp(-F_a - M)\} \qquad (5.20)$$

と定義した（Gabriel *et al.*, 1989）。ここで，fr_aはa歳の雌の成熟率でTable 3.12の値を使用した。YPR曲線の推定にあたりa歳における各地区の漁獲係数は，最近年のFの年齢別の選択率を使用した。価格の高い大型魚の期待漁獲重量を調べるため3歳以上のYPRについても調べた。生物学的資源管理基準値として$F_{0.1}$（Gulland and Boerema, 1973）と$F_{x\%SPR}$（x=30, 40, 50）（Mace, 1994）を求め，最近年2003年の漁獲係数$F_{current}$と比較した。また，各年齢の選択率を変化させ，若齢魚にかかる漁獲圧の違いによる期待漁獲量の変化を調べた。現状の各年齢の選択率を±1歳ずらし，若齢魚の漁獲圧が現状より強まる場合と弱まる場合について，YPRと3歳以上のYPRを比較した。

結　果

Table 5.1に地区別漁法別に推定した年別年齢別漁獲尾数を示す。Table 5.2はチューニングVPAで求めた，各地区におけるFとqの最小2乗法で求めたパラメータ推定値と，シミュレーション結果の平均，標準誤差，変動係数である。Area 1, 2-2, 2-3ではパラメータの推定精度が高かったが，Area 2-1では他と比較して精度が低かった。Area 1, 2-1, 2-2, 2-3各地区における漁獲割合の平均は，それぞれ重量で0.30，0.25，0.31，0.33，尾数で0.20，0.19，0.23，0.23であった。Fig. 5.1は，各地区の資源量推定値と，その標準誤差を示す。いずれの地区においても直近2～3年の誤差が増大する傾向がみられる。Fig. 5.2はArea 1における神津島の建切網，利島から式根島の寄網，大島の刺網のCPUEの理論値と観測値の年変化を示す。また，Fig. 5.3はArea 2-1～2-3の各地区におけるCPUEの理論値と観測値の年変化を示す。伊豆諸島北部海域の1998～2003年の資源量は，仮説1，仮説2どちらの場合も600～700t台を推移している。Fig. 5.4は各地域における，CPUEの実測値と理論値の標準化残差プロットを示す。Table 5.3は各地区における年別年齢別資源尾数，資源重量，漁獲係数の推定値を示す。

Fig. 5.5は各地区の自然死亡係数Mについて，感度解析を行った結果である。Mの値を現状より20%増加させると資源量が1.1～1.2倍に増加し，20%減少させると資源量が0.85～0.88倍に減少したが，資源の増減傾向は変わらなかった。Fig. 5.6は，Area 2-3についてレトロスペクティブ解析を行った結果である。最近年の推定値に一定の傾向は見られなかった。Fig. 5.7は耳石と鱗の年齢査定の読み取り誤差が資源量推定値に与える影響を，各年の資源重量（a）と，最近年2003年の年齢別資源重量（b）の変動係数を比較した結果である。資源重量推定値の変動係数は耳石，鱗いずれの読み取り誤差を考慮した場合でも同様の傾向を示すが，耳石を使用した方が推定精度は高いことを示す。また，Fig. 5.8は鱗の年齢組成の偏りを耳石の基準に変換した場合と，変換しない場合の年齢組成から求めた資源量推定値である。鱗のみの年齢組成情報では，耳石を使用した場合と比較して，資源量が2割ほど過小に推定された。

Table 5.4は各地区における生物学的資源管理基準値での漁獲係数，YPR, SPR, %SPRを示す。Fig. 5.9に2003年の選択率における漁獲係数に対する，%SPRとYPR，3歳以上（大型魚）のYPRの変化を示す。$F_{current}$は$F_{0.1}$に近い値であり，各地区の%SPRは2003年の漁獲圧で48.2%～52.1%だった。YPR解析の結果，

Table 5.1. Catch at age of each area and fishing gear.

Age area / fishing gear	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Area 2-1 / Gill net										
1	87,839	24,209	49,902	78,123	80,481	3,695	28,776	4,669	21,015	16,229
2	135,585	28,444	34,365	53,629	94,749	17,279	40,133	19,609	32,585	25,591
3	144,175	33,139	23,277	29,024	40,176	23,134	34,902	52,758	27,390	19,350
4	99,939	27,698	16,671	19,173	17,897	20,484	20,893	47,623	27,154	17,477
5+	42,872	16,138	9,828	9,954	4,454	17,499	7,525	16,808	14,167	17,477
Area 2-1 / Set net										
1	2,941		5,143		925	1,627	870	11,986	8,472	7,376
2	4,326		3,171		4,964	2,703	1,666	8,249	8,472	6,712
3	3,989		3,811		8,965	1,689	1,242	7,733	13,314	4,998
4	2,634		2,774		7,846	983	729	2,836	5,245	3,761
5+	1,245		1,456		5,506	465	339	644	0	2,512
Area 2-2 / Seine										
1		27,202			298,847	88,067	40,933	89,252	70,443	33,744
2		93,971			304,485	126,733	79,334	116,401	101,469	66,975
3		151,570			116,019	77,175	70,963	69,375	71,204	52,913
4		108,528			48,595	42,379	45,803	38,849	41,084	31,796
5+		45,484			10,934	20,443	24,797	15,142	15,666	13,174
Area 2-2 / Gill net										
1	47,263	91,074	138,942	158,045	254,481	42,037	121,265	147,612	167,932	83,596
2	138,170	198,573	95,684	209,216	245,140	74,323	133,310	190,473	158,067	131,704
3	270,534	203,776	64,810	118,763	102,929	56,066	108,821	125,732	85,998	117,365
4	201,866	137,866	46,416	83,007	49,683	42,363	75,959	79,735	45,128	84,659
5+	89,197	56,643	27,363	56,350	19,492	36,225	49,663	52,579	15,241	49,908
Area 2-3 / Bulk net										
1	81,455	33,106	46,367	109,868	201,628	67,219	126,292	188,342	137,411	42,985
2	153,824	90,215	70,360	93,116	472,885	189,309	98,589	336,914	197,932	252,950
3	243,952	184,223	95,857	55,129	211,294	134,522	55,705	166,823	138,896	145,487
4	189,492	166,508	89,797	40,645	101,818	71,907	35,102	87,911	80,141	66,131
5+	95,885	104,388	66,433	27,967	43,088	27,459	21,593	36,780	30,559	11,573
Area 2-3 / Gill net										
1	1,420	4,367	4,096	10,852	15,472	570	3,476	11,985	12,561	22,116
2	4,152	9,521	2,821	14,365	14,904	1,007	3,822	15,465	11,823	34,844
3	8,130	9,771	1,911	8,155	6,258	760	3,120	10,209	6,433	31,050
4	6,066	6,611	1,368	5,700	3,021	574	2,178	6,474	3,376	22,398
5+	2,680	2,716	807	3,869	1,185	491	1,424	4,269	1,140	13,204

Table 5.2. Point estimate, mean of simulation, standard error and coefficient of variance of the VPA parameters of each area.

		Fishing coefficient ($F_{4,2003}$)	Catchability		
			Gill net	Seine	Bulk net
Area 1	Point estimate	0.626	0.00084	0.00229	0.00281
	Mean of simulation	0.641	0.00079	0.00229	0.00279
	SE	0.139	0.00017	0.00026	0.00043
	CV	0.22	0.22	0.11	0.15
Area 2-1	Point estimate	0.631	0.00497		
	Mean of simulation	0.749	0.00536		
	SE	0.375	0.00132		
	CV	0.50	0.25		
Area 2-2	Point estimate	0.741		0.00490	
	Mean of simulation	0.709		0.00469	
	SE	0.115		0.00040	
	CV	0.16		0.08	
Area 2-3	Point estimate	1.048			0.01011
	Simulation mean	0.966			0.00952
	SE	0.175			0.00073
	CV	0.18			0.08

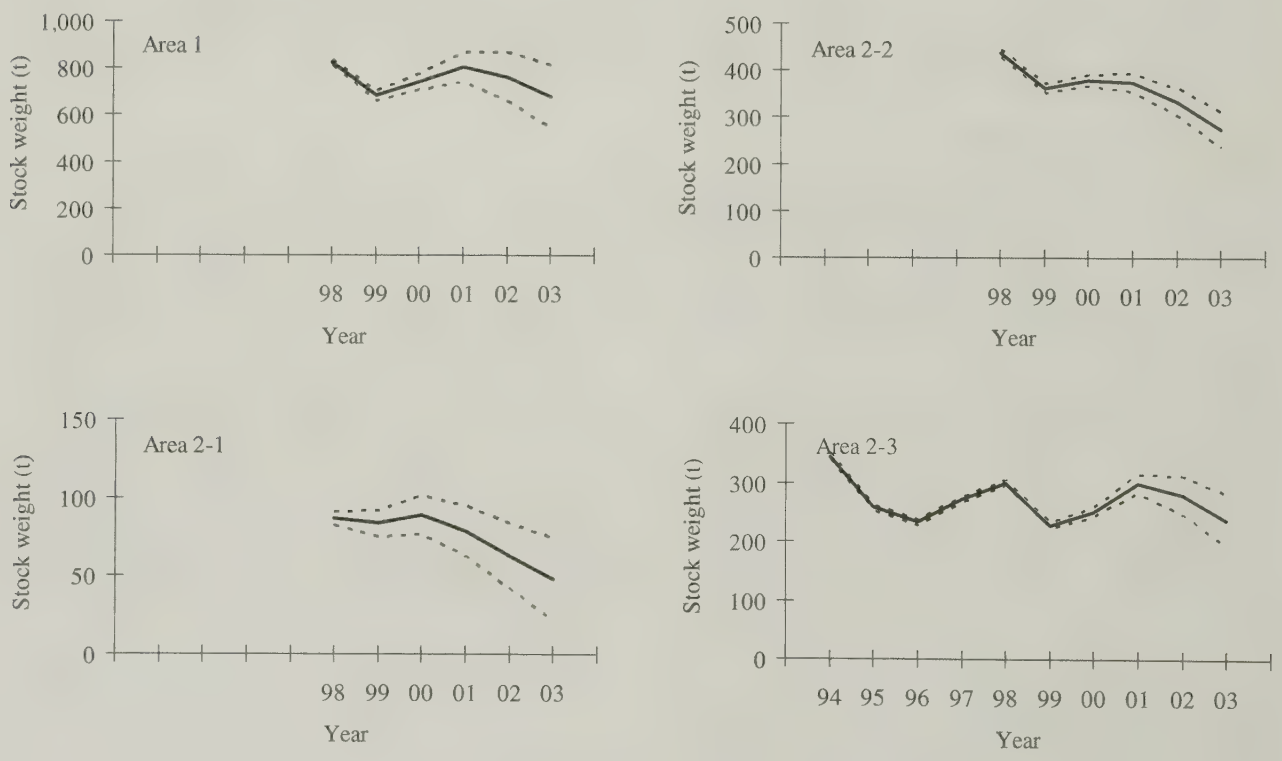

Fig. 5.1. Estimated stock weight of butterfish. Solid and dotted lines indicate point estimate and standard error, respectively.

漁獲圧を現状より高めると，小型魚の漁獲量はわずかに増えるものの，大型魚の漁獲の増加は期待できず，減少する危険があることを示す。Fig. 5.10は，各地区における若齢魚に対する漁獲圧を現状より高めた場合と低下させた場合のYPRと3歳以上の期待漁獲量の比較である。各地区とも現状の漁獲係数のもとでは，若齢魚の漁獲圧を増大させても，全体の漁獲量はほとんど変わらないが，大型魚の漁獲量が減少することが示された。

考　察

最近年の資源量推定値は，資源管理上最も重要な情報であるが，推定値の誤差が大きかった。しかしながら，レトロスペクティブ解析結果が示すように，最近年の推定値にモデルに起因する偏りは見られない。最近年のターミナルFの推定方法として，1～4歳のFを全て未知パラメータとした場合も試みた。しかし，データに漁獲圧の低い若齢の年級に関する情報が，ほとんど含まれていないと考えられるため，1，2歳部分の資源量がうまく推定できなかった。各年齢にかかる漁獲圧は，高齢部と比較して1，2歳が低くなる傾向がいずれの年も共通に見られる。解析期間中に漁獲の形態などが大きく変化していないため，最近年の選択率が過去数年の平均であると仮定する方法を用いても，Fは十分に推定できるものと考えられる。

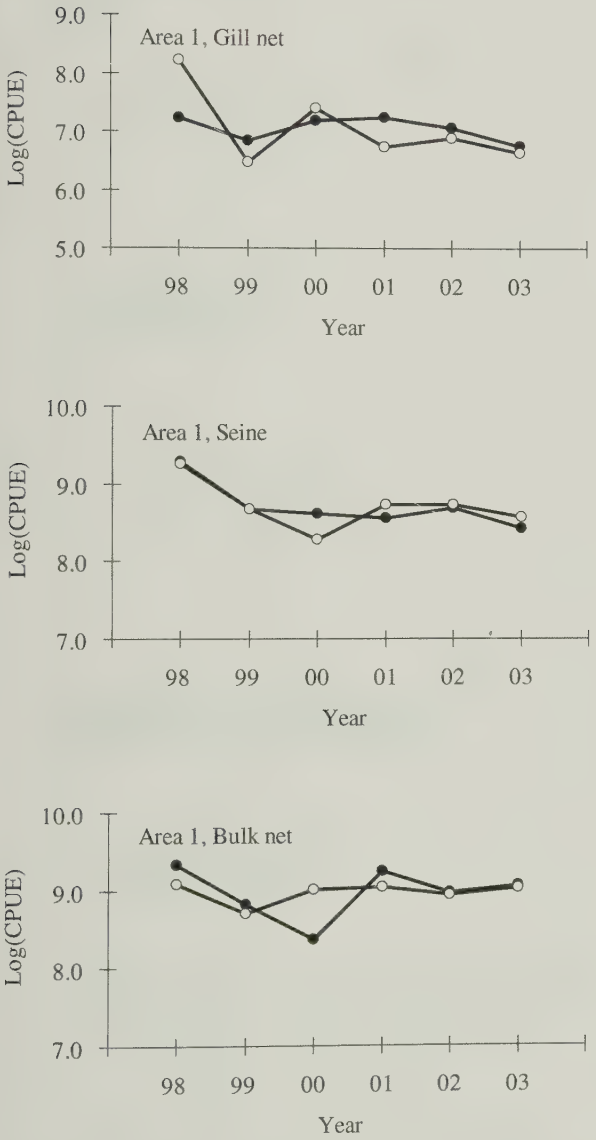

Fig. 5.2. Comparison of the expected value of the log CPUE (open circles) and the observed one (black ones) in area 1.

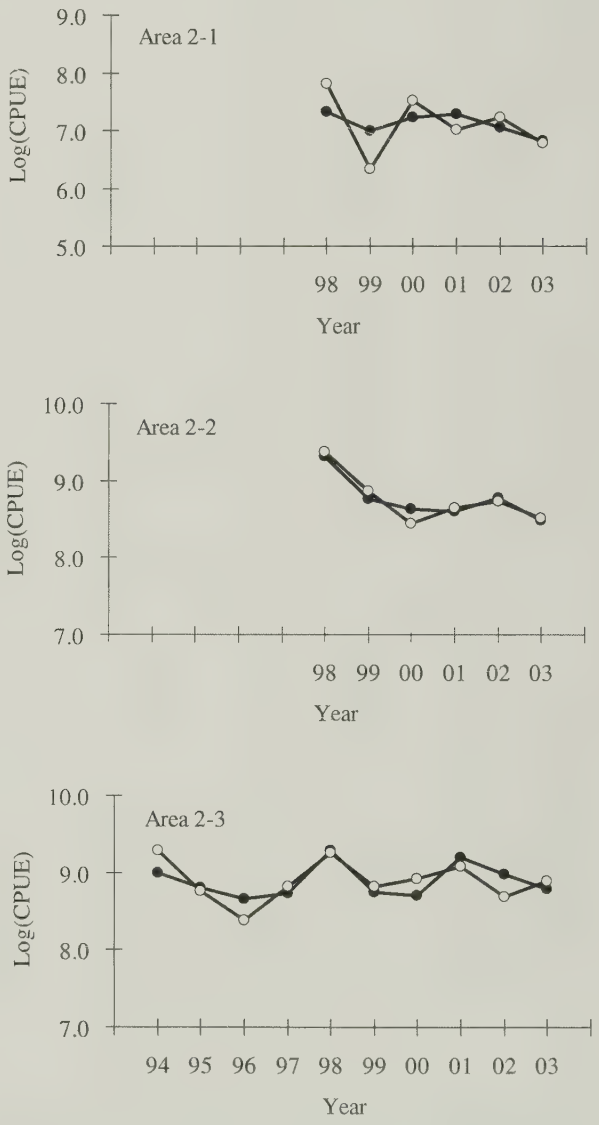

Fig. 5.3. Comparison of the expected value of the log CPUE (open circles) and the observed one (black ones) in area 2-1, 2-2, and 2-3.

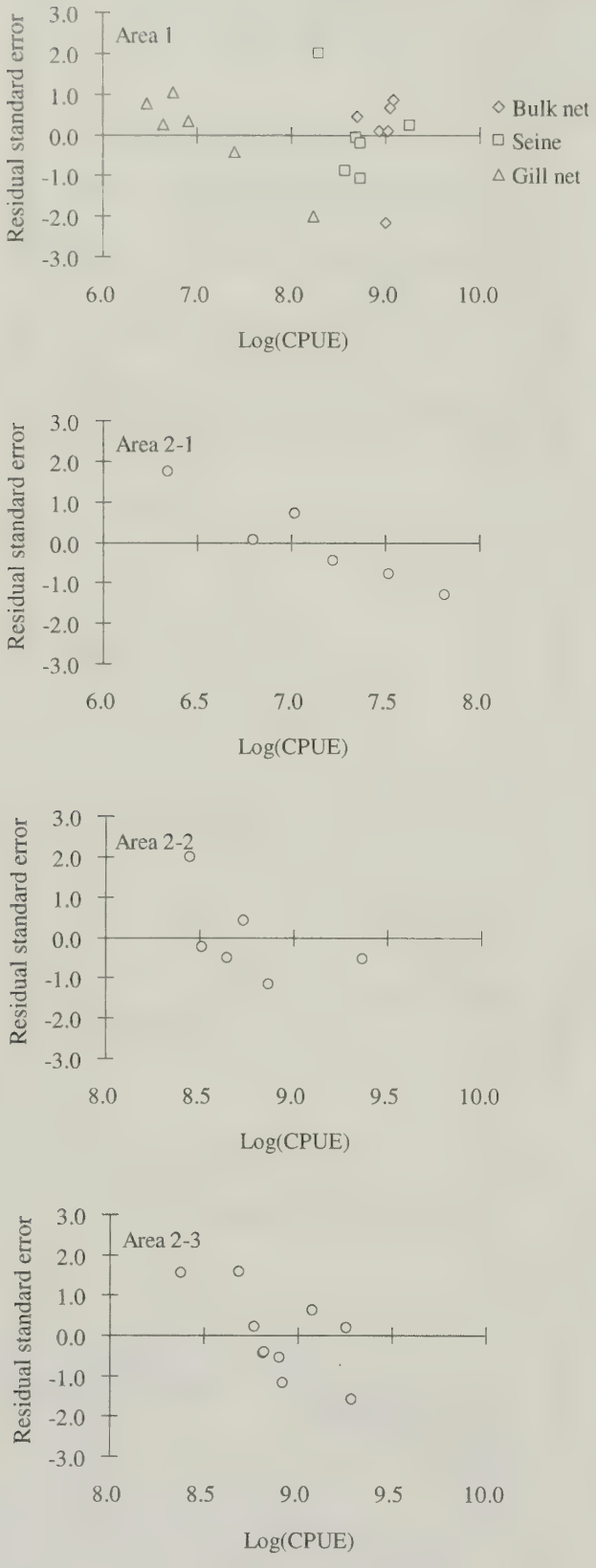

Fig. 5.4. Plot of the residual standard error against the log CPUE of each area.

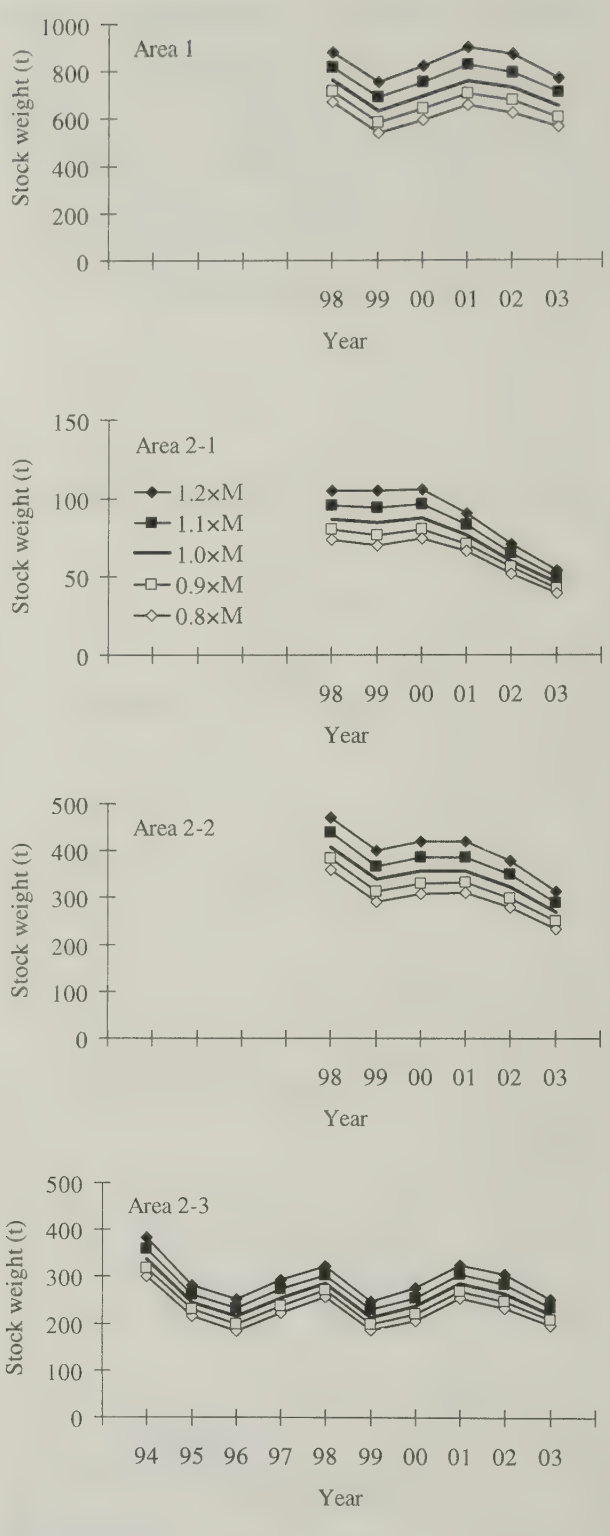

Fig. 5.5. Results of the sensitivity tests of the values for natural mortality coefficient of each area.

Table 5.3. The estimated stock number and weight at age, total fishing mortality and fishing mortality of the each fishery and area.

Area 1	Age	1998	1999	2000	2001	2002	2003
Stock number at age	1	3,996,197	3,547,251	4,056,777	4,166,768	3,901,505	2,135,355
	2	2,805,903	2,093,316	2,313,185	2,571,604	2,540,370	2,383,830
	3	1,263,796	1,034,009	1,123,393	1,321,611	1,232,508	1,355,134
	4	581,411	487,084	481,880	559,206	570,375	582,525
	5+	220,969	299,752	303,636	297,338	259,857	332,263
Stock weight at age (t)	1	207	184	210	216	202	111
	2	317	237	261	291	287	269
	3	164	135	146	172	160	176
	4	78	65	65	75	76	78
	5+	30	40	41	40	35	45
Fishing coefficient (total)	1	0.289	0.070	0.099	0.138	0.136	0.121
	2	0.641	0.265	0.203	0.378	0.271	0.297
	3	0.596	0.406	0.340	0.483	0.392	0.389
	4	0.627	0.595	0.614	0.836	0.559	0.626
	5+	0.627	0.595	0.614	0.836	0.559	0.626
Fishing coefficient (bulk net)	1	0.069	0.023	0.039	0.057	0.045	0.025
	2	0.267	0.122	0.056	0.185	0.105	0.145
	3	0.260	0.186	0.069	0.187	0.160	0.152
	4	0.282	0.230	0.117	0.273	0.219	0.178
	5+	0.332	0.140	0.115	0.217	0.199	0.094
Fishing coefficient (seine)	1	0.102	0.031	0.013	0.027	0.023	0.020
	2	0.172	0.082	0.045	0.064	0.054	0.038
	3	0.142	0.107	0.088	0.078	0.082	0.055
	4	0.131	0.140	0.154	0.124	0.112	0.087
	5+	0.078	0.118	0.139	0.107	0.102	0.066
Fishing coefficient (gill net : Oshima island)	1	0.027	0.001	0.009	0.001	0.007	0.010
	2	0.053	0.011	0.023	0.011	0.017	0.015
	3	0.049	0.032	0.043	0.059	0.032	0.020
	4	0.048	0.074	0.068	0.146	0.073	0.047
	5+	0.032	0.120	0.040	0.126	0.107	0.112
Fishing coefficient (set net)	1	0.000	0.001	0.000	0.003	0.003	0.004
	2	0.003	0.002	0.001	0.004	0.005	0.004
	3	0.011	0.002	0.002	0.007	0.011	0.005
	4	0.022	0.003	0.002	0.013	0.018	0.010
	5+	0.042	0.003	0.002	0.011	0.014	0.012
Fishing coefficient (gill net : others)	1	0.092	0.015	0.038	0.049	0.059	0.062
	2	0.147	0.049	0.078	0.114	0.090	0.096
	3	0.134	0.079	0.139	0.152	0.107	0.156
	4	0.143	0.148	0.272	0.280	0.137	0.303
	5+	0.144	0.215	0.317	0.374	0.136	0.342

Table 5.3. (*Continued*)

Area 2-1	Age	1998	1999	2000	2001	2002	2003
Stock number at age	1	565,503	504,423	326,362	249,279	248,454	165,609
	2	328,015	328,308	348,504	203,763	161,664	149,722
	3	129,964	147,539	212,586	209,186	119,673	79,141
	4	80,891	50,727	82,502	118,856	97,613	53,228
	5+	32,273	49,226	30,912	54,702	59,608	65,507
Stock weight at age (t)	1	27	24	15	12	12	8
	2	33	33	36	21	16	15
	3	15	17	25	25	14	9
	4	10	6	10	14	12	6
	5+	4	6	4	7	7	8
Fishing coefficient (total)	1	0.187	0.013	0.114	0.076	0.149	0.185
	2	0.442	0.077	0.153	0.175	0.357	0.294
	3	0.584	0.224	0.224	0.405	0.453	0.448
	4	0.475	0.816	0.372	0.712	0.518	0.631
	5+	0.475	0.816	0.372	0.712	0.518	0.631
Fishing coefficient (gill net)	1	0.184	0.009	0.111	0.023	0.108	0.127
	2	0.419	0.067	0.147	0.124	0.282	0.233
	3	0.477	0.209	0.217	0.360	0.334	0.356
	4	0.326	0.783	0.359	0.652	0.418	0.517
	5+	0.203	0.799	0.355	0.653	0.458	0.570
Fishing coefficient (set net)	1	0.002	0.004	0.003	0.053	0.042	0.058
	2	0.022	0.010	0.006	0.051	0.075	0.061
	3	0.107	0.015	0.008	0.045	0.119	0.092
	4	0.149	0.034	0.013	0.059	0.101	0.114
	5+	0.272	0.017	0.017	0.059	0.061	0.061

Area 2-2	Age	1998	1999	2000	2001	2002	2003
Stock number at age	1	2,139,338	1,750,968	1,875,423	1,834,601	1,488,460	892,535
	2	1,442,640	1,041,356	1,117,149	1,177,660	1,087,507	844,327
	3	633,316	559,814	561,593	604,651	570,160	546,494
	4	321,252	263,727	281,663	244,969	262,600	269,328
	5+	97,730	187,543	189,932	154,149	114,088	158,197
Stock weight at age (t)	1	113	92	99	97	78	47
	2	164	119	127	134	124	96
	3	83	74	74	79	75	72
	4	43	36	38	33	36	36
	5+	13	26	26	21	16	22
Fishing coefficient (total)	1	0.363	0.092	0.108	0.166	0.210	0.169
	2	0.589	0.260	0.257	0.368	0.331	0.327
	3	0.519	0.330	0.473	0.477	0.393	0.456
	4	0.447	0.508	0.761	0.895	0.510	0.741
	5+	0.447	0.508	0.761	0.895	0.510	0.741
Fishing coefficient (seine)	1	0.196	0.062	0.027	0.062	0.062	0.049
	2	0.326	0.164	0.095	0.139	0.129	0.110
	3	0.275	0.191	0.186	0.170	0.178	0.142
	4	0.220	0.249	0.280	0.289	0.239	0.197
	5+	0.163	0.182	0.237	0.211	0.228	0.145
Fishing coefficient (gill net)	1	0.167	0.030	0.081	0.103	0.148	0.120
	2	0.263	0.097	0.161	0.229	0.202	0.217
	3	0.244	0.139	0.286	0.307	0.215	0.315
	4	0.227	0.259	0.482	0.606	0.272	0.544
	5+	0.284	0.326	0.524	0.684	0.282	0.596

Table 5.3. (*Continued*)

Area 2-3	Age	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Stock number at age	1	845,884	844,895	1,201,216	1,583,862	1,191,436	1,088,584	1,549,558	1,557,038	1,668,843	564,957
	2	862,050	523,139	560,021	798,534	1,008,024	654,271	705,378	976,545	923,551	1,043,278
	3	741,398	472,657	283,665	331,245	469,743	309,075	301,367	408,798	394,762	473,259
	4	410,642	312,108	172,350	118,355	179,505	151,698	106,016	162,292	141,726	157,271
	5+	206,973	193,092	127,119	81,304	75,804	58,496	65,455	70,582	53,793	44,016
Stock weight at age (t)	1	46	46	65	86	65	59	84	85	91	31
	2	101	61	66	94	118	77	83	114	108	122
	3	100	64	38	45	63	42	41	55	53	64
	4	57	43	24	16	25	21	15	23	20	22
	5+	29	27	18	11	11	8	9	10	8	6
Fishing coefficient (total)	1	0.123	0.054	0.051	0.095	0.242	0.077	0.105	0.165	0.113	0.147
	2	0.244	0.255	0.168	0.173	0.825	0.418	0.188	0.549	0.311	0.392
	3	0.508	0.652	0.517	0.256	0.773	0.713	0.262	0.702	0.563	0.573
	4	0.806	1.023	0.947	0.611	1.116	0.810	0.530	1.108	1.134	1.048
	5+	0.806	1.023	0.947	0.611	1.116	0.810	0.530	1.108	1.134	1.048
Fishing coefficient (bulk net)	1	0.121	0.048	0.047	0.086	0.225	0.076	0.102	0.155	0.103	0.097
	2	0.237	0.231	0.161	0.150	0.800	0.416	0.181	0.525	0.294	0.345
	3	0.492	0.619	0.507	0.223	0.751	0.709	0.248	0.662	0.538	0.472
	4	0.781	0.984	0.932	0.536	1.084	0.803	0.500	1.032	1.088	0.783
	5+	0.784	0.997	0.935	0.537	1.086	0.795	0.498	0.993	1.093	0.490
Fishing coefficient (gill net)	1	0.002	0.006	0.004	0.009	0.017	0.001	0.003	0.010	0.009	0.050
	2	0.006	0.024	0.006	0.023	0.025	0.002	0.007	0.024	0.018	0.047
	3	0.016	0.033	0.010	0.033	0.022	0.004	0.014	0.040	0.025	0.101
	4	0.025	0.039	0.014	0.075	0.032	0.006	0.031	0.076	0.046	0.265
	5+	0.022	0.026	0.011	0.074	0.030	0.014	0.033	0.115	0.041	0.559

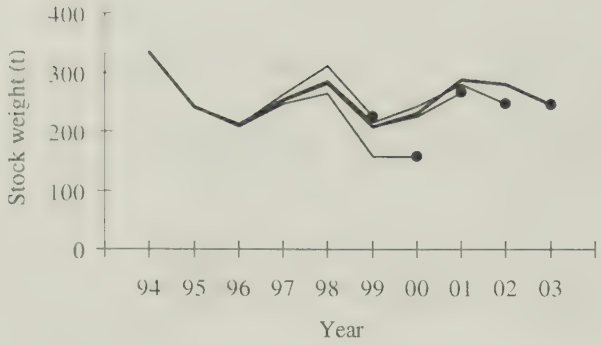

Fig. 5.6. Result of the retrospective analysis in area 2-3.

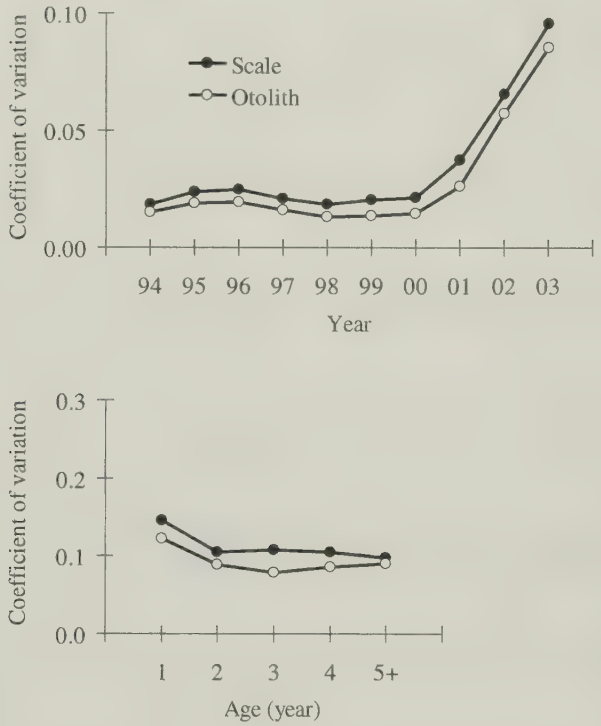

Fig. 5.7. Comparison of coefficient of variation from within ageing error of otolith and scale in area 2-3. (a) CV of stock weight from 1994 to 2003, (b) CV of stock weight at age in 2003.

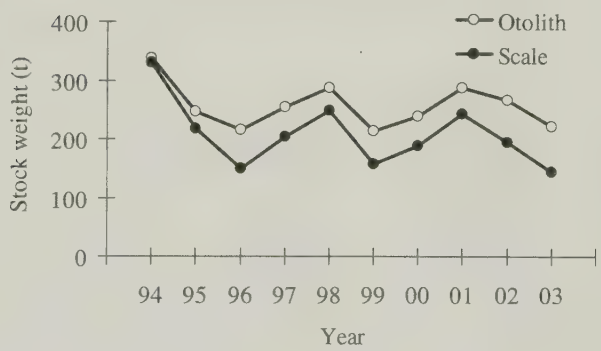

Fig. 5.8. Comparison of stock weight which estimated from age composition of otolith and scale in area 2-3.

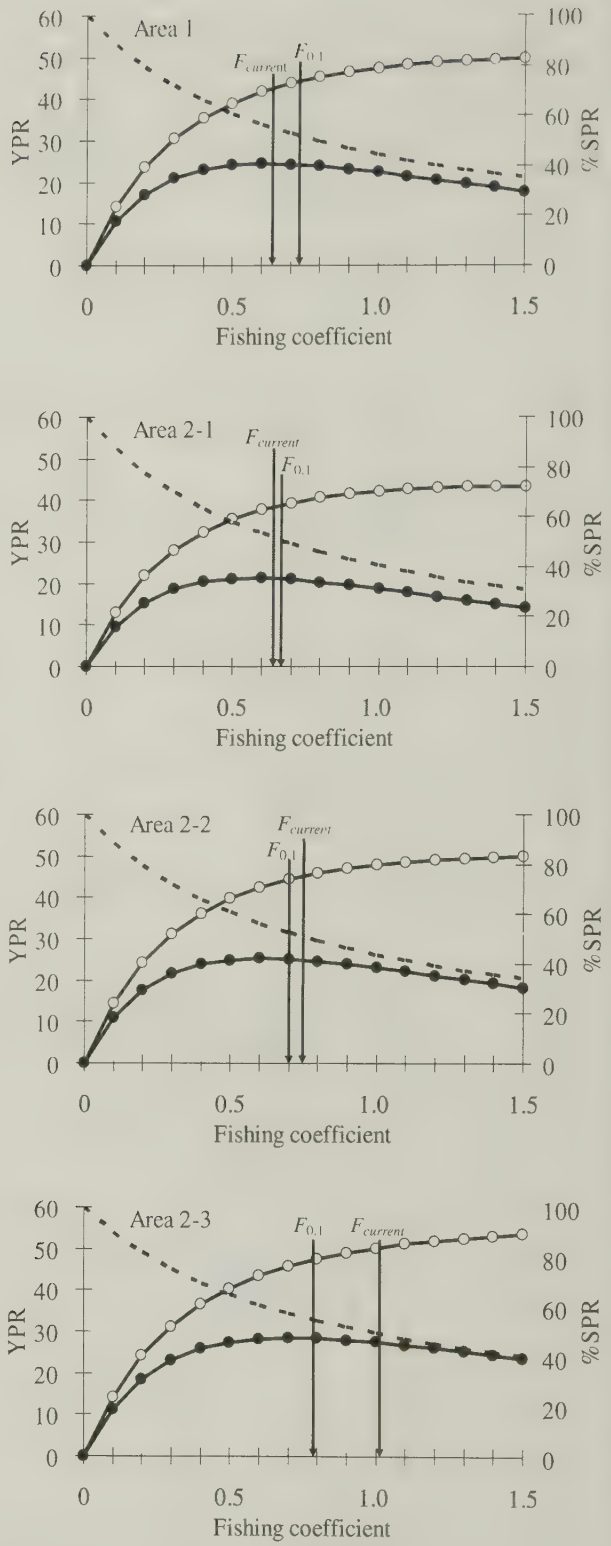

Fig. 5.9. YPR and %SPR at fishing coefficient of each area. Dotted lines, lines with open circle, and lines with black circle indicate %SPR, YPR, and YPR at age of 7 from 3, respectively.

Table 5.4. Results of fishing mortality, yield per recruitment and spawning biomass per recruit for biological reference points in area 1, 2-1, 2-2, and 2-3.

		$F_{current}$	$F_{0.1}$	$F_{50\%SPR}$	$F_{40\%SPR}$	$F_{30\%SPR}$
Area 1	F	0.63	0.72	0.79	1.20	1.90
	YPR	42.3	44.0	45.1	48.7	49.8
	SPR	144.6	136.3	130.4	104.3	78.2
	%SPR	55.5	52.3	50.0	40.0	30.0
Area2-1	F	0.63	0.66	0.68	1.01	1.54
	YPR	38.3	38.7	39.1	42.2	43.3
	SPR	121.7	119.4	117.2	93.8	70.3
	%SPR	51.9	50.9	50.0	40.0	30.0
Area2-2	F	0.74	0.70	0.77	1.16	1.79
	YPR	45.1	44.4	45.4	48.9	50.0
	SPR	136.8	140.5	134.6	107.6	80.7
	%SPR	50.8	52.2	50.0	40.0	30.0
Area2-3	F	1.05	0.79	0.97	1.52	2.48
	YPR	50.8	47.4	49.9	53.6	54.7
	SPR	135.4	153.8	140.4	112.3	84.3
	%SPR	48.2	54.8	50.0	40.0	30.0

資源量推定は，Area 2-3で10年間のデータを用いて解析を行ったが，他の地区では6年間の解析しか実施しておらず，解析期間の短さが資源量推定結果に影響を与えている可能性がある。レトロスペクティブ解析の結果は，1994～1999年など期間が短くても，資源量の推定値や変動に偏りが生じていないことを示している(Fig. 5.6)。Area 2-3以外は短期間の解析であるが，近年の漁獲量やF，漁獲率など漁業の現状評価について利用可能な情報をもたらす。

年別年齢別漁獲尾数の推定において，資源量推定値の偏りをなくし，推定精度を維持する両面から，鱗より耳石を使用する方が良いと考えられる。しかし，耳石標本を大量に処理することは，費用と時間の両面から実施が困難な場合も考えられる。このため，一部個体を耳石と鱗両方査定し，残りを鱗のみ年齢査定を行い，耳石の査定基準に変換する方法も有効である。また，簡便な方法として，体長組成を計測した標本から一部を抽出し年齢査定を行う，二段サンプリング（田中，1960；Lai, 1987）や，Age-length key による年齢割合の推定についても検討した。しかし，2段サンプリングの場合，体長階級内の分散と体長階級間の分散を比較すると，体長階級内の分散が大きく，体長の層別の効果がほとんど無かった。漁獲対象サイズ前の小型魚は，成長が速いため体長組成から十分年齢査定可能である（Fig. 2.6)。しかし，漁獲対象となってからは，成長が緩やかなため体長が持つ年齢の情報は少ない。

本研究では，年齢査定を1人の査定者が実施したため，資源量推定値に与える年齢査定に関わる誤差として，同一査定者による輪紋読み取り誤差のみを考慮したが，今後複数の査定者により年齢査定が行われる場合，査定者間の誤差も考慮する必要が生じると予想される（Kimura and Lyons, 1991；Eklund, 2000)。査定者間の輪紋数査定値の偏りが大きい場合，年齢組成に偏りが生じ，耳石と鱗の間の偏りと同様に，資源量推定値にも影響を及ぼす可能性がある。今後新たな査定者により輪紋数の計測が実施される場合，輪紋の判定基準の維持と統一に努めるとともに，査定者間の偏りの有無の評価（Richards *et al.*, 1992）も実施する必要がある。

資源量や漁獲率，選択率などの解析結果は，移動の仮説によらず，同様の傾向を示した。漁獲の多いArea 2-2と2-3で，漁獲対象としているサイズや，操業の形態や期間などに類似点が多いため，北部海域全体で解析を行っても，地区ごとに解析を行っても，あまり差が生じないもと思われる。このため同海域における，タカベ資源の現状評価や管理方策の検討にあたっては，移動の仮説に関わらず同様の判断が可能と考

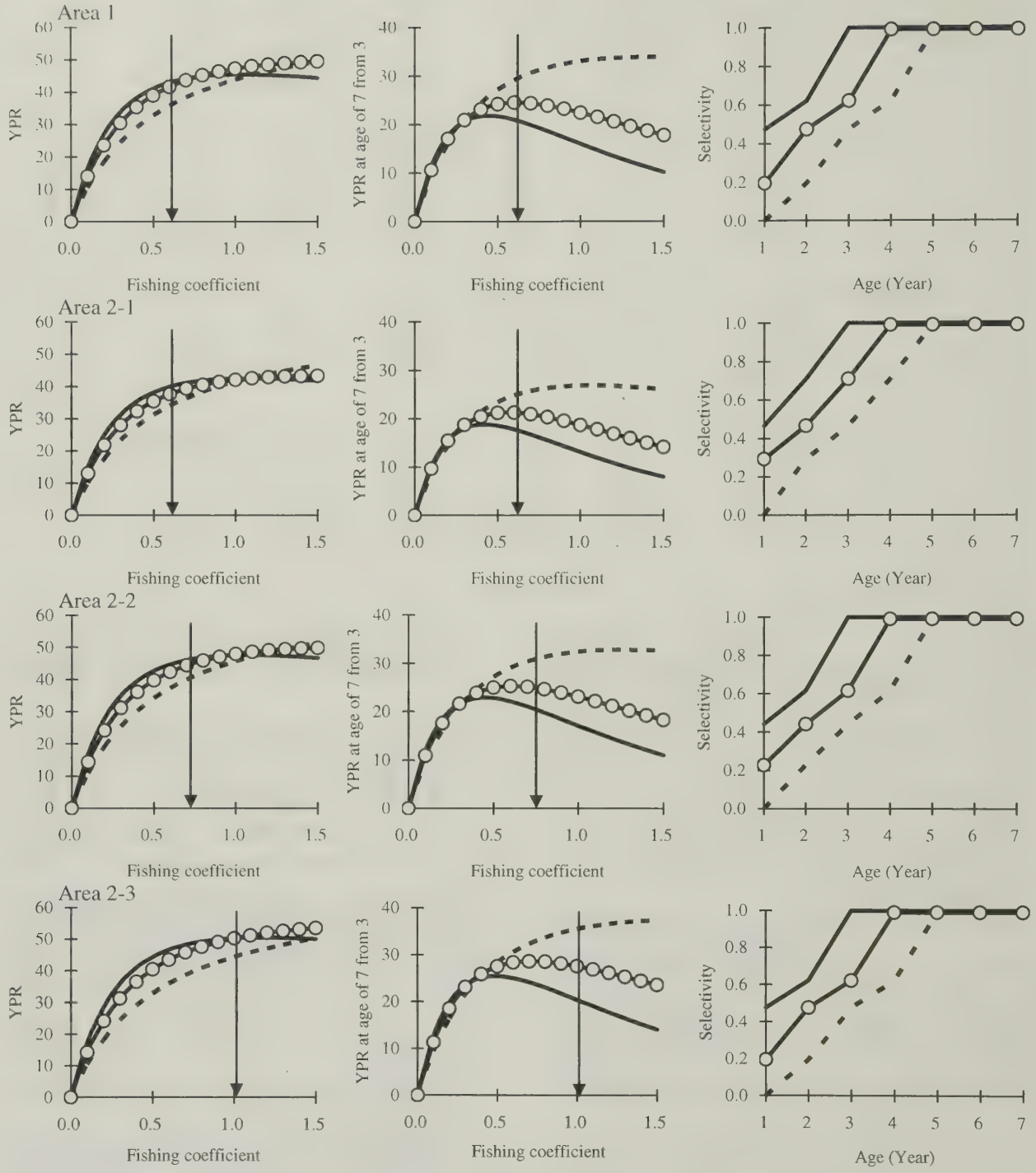

Fig. 5.10. Comparison of YPR and YPR at age of 7 from 3 by three patterns of selectivity of each area. Open circle indicate current case. The allows indicate $F_{current}$.

えられる。

F%SPR は加入乱獲の閾値として用いられ，20～30% の値が提唱されている（Goodyear, 1993 ; Mace and Sissenwine, 1993）。同海域においては，いずれの地区でも %SPR の値が50程度であることから，加入乱獲で危険な状態になっていない。また，現状の漁獲係数 $F_{current}$ と $F_{0.1}$ が近い値であり，当地域のタカベ漁業の漁獲圧は過剰ではないと考えられる。年齢別漁獲係数の推定結果は，ほとんどの年，地区において，若齢の漁獲圧が高齢と比較して低いことを示している。このことは，伊豆諸島北部海域において，高齢のタカベが中心に漁獲されていることを意味する。しかし，操業実態が変化し若齢の漁獲圧が高まった場合，大型魚の期待漁獲量，SPR ともに減少することが示唆されている。このため，タカベの管理においては生物学的資源管理基準と現状の F との比較だけでなく，年齢やサイズと漁獲の関係についても，同時に注目する必要がある。特に漁獲物に占める小型魚の割合が増加した場合，それが卓越年級群の出現によるのか，若齢魚に対する漁獲圧の増大によるのか的確に把握することは，タカベ資源の持続的利用の確保にとって重要な課題である。

資源量推定を行った期間が短いことと，この期間に資源水準が大きく変動していないため，本研究結果から再生産関係を把握することができなかった。神津島周辺海域では，1998年の資源量が多く，その中で２歳魚の割合が高いことから，1996年生まれの加入量が多かったと考えられる。また，1998年は他の地区においても２歳魚の漁獲割合が高いことから，1996年生まれは伊豆諸島北部海域全体で加入が良かったものと推測できる。しかし，神津島において1996年の産卵親魚となる２歳以降の資源量は，他年と比較して多いわけではない（Table 5.3）。小達1962は，伊豆諸島周辺海域で孵化したタカベの仔稚魚が，黒潮により東北海区常磐沖まで拡散することを報告している。また，タカベの仔稚魚が伊豆諸島より西部の和歌山県沖で採取されている（堀木，1975）ことに加え，伊豆諸島北部海域のタカベと愛媛で捕獲されたタカベの集団間に遺伝的差異がない（東京都水産試験場資源管理部，2004）ことが示している。これらの点から，伊豆諸島で生まれたタカベが，他の海域へ流出することや，他の海域で生まれたタカベが，伊豆諸島海域へ流入することが考えられる。伊豆諸島海域での加入量は，単純に同海域の親子関係のみで決定できず，黒潮流路や潮流などの海洋環境との関わりもあると考えられる。資源と環境要因の関係や再生産関係の把握は今後の課題としたい。

第六章　総合考察

本研究により，伊豆諸島北部海域におけるタカベ資源の年齢と成長の把握や CPUE 標準化，資源量推定を行い，資源の現状評価と管理に関する情報を得ることができた。同海域での推定資源量は，近年600~700t 台で推移しているが，1960年代に現状の資源量を上回る700t 以上の漁獲が続いた。当時の操業は，大島から神津島の周辺海域に加え，銭洲周辺海域でも頻繁に行われており，漁場の範囲が現在より広かったことが要因の１つであるが，伊豆諸島周辺海域においてタカベ資源が現在より高位水準で存在していたものと考えられる。1960年代と比較すると，近年の資源は低位水準であるが，1991年以降 CPUE に増減傾向は見られず横ばいであることが示された。また，$F_{current}$ と $F_{0.1}$ が近い値であることと，YPR，SPR 解析の結果を踏まえると，現在のタカベ資源の漁獲圧は過剰でないと考えられる。同海域のタカベ資源が比較的安定している要因として，小型魚の漁獲が抑えられていることが挙げられる。

漁獲開始年齢は１歳半で，ある程度成長したタカベが漁獲されていることがわかった。また，資源解析で得られた年齢と選択率の関係から，漁獲開始年齢以降しばらくの間は，高齢魚と比較して漁獲圧が低いことも示された。市場では大型のタカベの方が高値で取引されるため，建切網や寄網では，人為的な選択により小型魚の獲り控えが行われていると考えられる。同海域の天然のタカベ資源において，小型魚の獲り残しを可能にする背景として，現在タカベを中心に漁獲する経営体が，伊豆諸島各島でそれぞれ１～３程度しかないことが挙げられる。加入資源に対して，先取り競争に陥らず，有効的な利用が行われているものと考えられる。

YPR 解析の結果，漁獲圧を現状より低下させても，漁獲量の増加は期待できないことを示している。また，現状より漁獲圧を高めた場合，期待漁獲量が大幅に増加しないことに加え，資源に与える影響が小さいという十分な証拠も得られていない。現在の加入量水準のもとで，タカベ資源の持続的利用のためには，現状の努力量と若齢魚に対する低い漁獲圧の両方を維持する必要がある。

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Appendix A

Program of Visual Basic for Applications (VBA) used for the tuning VPA.

```
Sub VPA()

Randomize
Worksheets("data input").Activate

    Dim C() As Double
    Dim Csum() As Double
    Dim Cse() As Double
    Dim N() As Double
    Dim Na() As Double
    Dim Nave() As Double
    Dim q() As Double
    Dim F() As Double
    Dim Fa() As Double
    Dim Fb() As Double
    Dim Fans() As Double
    Dim Feach() As Double
    Dim LnCPUE() As Double
    Dim CPUEcv() As Double
    Dim cpueORG() As Double
    Dim aveW() As Double

    Dim YrSSQ() As Double
    Dim Yr As Integer
    Dim Ag As Integer
    Dim Series As Integer
    Dim i As Integer
    Dim j As Integer
    Dim k As Integer

    Dim x() As Double
    Dim Fssq() As Double
    Dim x0() As Double
    Dim Xhigh() As Double
    Dim xSecond() As Double
    Dim Xsmall() As Double
    Dim xr() As Double
    Dim xe() As Double
    Dim xc() As Double

    Dim fHigh As Double
    Dim fSecond As Double
    Dim fSmall As Double
    Dim fr As Double
    Dim fe As Double
    Dim fc As Double
    Dim fAve1 As Double
    Dim fAve2 As Double

    Dim aa As Double
    Dim paraNum As Integer
    Dim fBefore As Double
    Dim Fseries() As Double
```

```
    Dim paraMeter() As Double
    Dim CatchNum As Integer
    Dim CdataNum As Double

    Dim qCons As Double
    Dim FaMax() As Double
    Dim S() As Double
    Dim SN() As Double
    Dim Fgroup() As Integer
    Dim d As Double
    Dim CPUEresid() As Double
    Dim se() As Double

Worksheets("model_info").Activate
      CPUEweight = ActiveSheet.Cells(10, 2)
      terminalF = ActiveSheet.Cells(13, 2)
      alpha = ActiveSheet.Cells(15, 2)
      selectivityPattern = ActiveSheet.Cells(18, 2)
      backYr = ActiveSheet.Cells(20, 2)
      bootmode = ActiveSheet.Cells(22, 2)
      bootNum = ActiveSheet.Cells(24, 2)

Worksheets("data input").Activate
    AgeNum = ActiveSheet.Cells(6, 4)
    YrNum = ActiveSheet.Cells(4, 4)
    CatchNum = ActiveSheet.Cells(8, 2)
    qNum = ActiveSheet.Cells(8, 3)
    paraNum = 1 + qNum

    ReDim C(AgeNum, YrNum, CatchNum) As Double
    ReDim Csum(AgeNum, YrNum) As Double
    ReDim Cse(AgeNum, YrNum, CatchNum) As Double
    ReDim N(AgeNum, YrNum) As Double
    ReDim Na(AgeNum, YrNum) As Double
    ReDim Nave(AgeNum, YrNum) As Double
    ReDim q(CatchNum) As Double
    ReDim F(AgeNum, YrNum) As Double
    ReDim Fa(AgeNum, YrNum) As Double
    ReDim Fb(AgeNum, YrNum) As Double
    ReDim Fans(AgeNum, YrNum) As Double
    ReDim Feach(AgeNum, YrNum, CatchNum) As Double
    ReDim LnCPUE(YrNum, CatchNum) As Double
    ReDim CPUEcv(YrNum, CatchNum) As Double
    ReDim YrSSQ(YrNum) As Double
    ReDim aveW(AgeNum) As Double

    ReDim paraMeter(paraNum) As Double
    ReDim x(paraNum + 1, paraNum) As Double
    ReDim Fssq(paraNum + 1) As Double
    ReDim x0(paraNum) As Double
    ReDim Xhigh(paraNum) As Double
    ReDim xSecond(paraNum) As Double
    ReDim Xsmall(paraNum) As Double
    ReDim xr(paraNum) As Double
    ReDim xe(paraNum) As Double
    ReDim xc(paraNum) As Double

    ReDim FaMax(YrNum, CatchNum) As Double
    ReDim S(AgeNum, YrNum, CatchNum) As Double
```

```
ReDim SN(YrNum, CatchNum) As Double
ReDim CPUEresid(Yr, CatchNum)
ReDim CPUEse(CatchNum)

Select Case bootmode
Case Is = 0      'VPA パラメータ点推定
    GoSub DataSet                       'データ入力
    GoSub Simplex                       'パラメータ最適化
    GoSub VPA1
    GoSub OutPut                        'データ出力

Case Is = 1      'Bootstarp CPUE
    GoSub DataSet

    For bt = 1 To bootNum
        GoSub BootDataInput_CPUE        'ブートストラップデータ入力(CPUE)
        GoSub Simplex                   'パラメータ最適化
        GoSub VPA1
        GoSub BootOutPut                'データ出力
    Next bt

Case Is = 2      'VPA で資源量推定→CPUE で bootstrap
    GoSub DataSet                       'データ入力
    GoSub Simplex                       'パラメータ最適化
    GoSub VPA1
    GoSub OutPut                        'データ出力
    GoSub BootSample_CPUE               'ブートストラップサンプル(CPUE)作成

    For bt = 1 To bootNum
        GoSub BootDataInput_CPUE        'ブートストラップデータ入力(CPUE)
        GoSub Simplex                   'パラメータ最適化
        GoSub VPA1
        GoSub BootOutPut                'データ出力
    Next bt

Case Is = 3      'Catch の bootstrap Catch データは外部入力
    GoSub DataSet                       'データ入力

    For bt = 1 To bootNum
        GoSub BootDataInput_Catch       'ブートストラップデータ入力(Catch)
        GoSub Simplex                   'パラメータ最適化
        GoSub VPA1
        GoSub BootOutPut                'データ出力
    Next bt

Case Is = 4      'VPA で資源量推定→CPUE と Catch で bootstrap Catch データは外部入力
GoSub DataSet                           'データ入力
GoSub Simplex                           'パラメータ最適化
GoSub VPA1
GoSub OutPut                            'データ出力
GoSub BootSample_CPUE                   'ブートストラップサンプル(CPUE)作成

    For bt = 1 To bootNum
        GoSub BootDataInput_CPUE        'ブートストラップデータ入力(CPUE)
        GoSub BootDataInput_Catch       'ブートストラップデータ入力(Catch)
        GoSub Simplex                   'パラメータ最適化
        GoSub VPA1
        GoSub BootOutPut                'データ出力
    Next bt
```

```
    Case Is = 5      'VPA パラメータ点推定
    For retro = 1 To 5
        GoSub DataSet      'データ入力
        GoSub Simplex      'パラメータ最適化
        GoSub VPA1
        GoSub OutPut       'データ出力
        GoSub Retros       'レトロスペクティブ解析の結果表示
    Next retro
    End Select

    Exit Sub

VPA1:
    If terminalF = 1 Then GoSub VPA_Fmax_year_const
    If terminalF = 2 Then GoSub VPA_Fmax_age_const
Return


'#MENU#
   ↓
'VPA データ入力
'Simplex 法(非線形最適化)
'VPA, 目的関数の計算
'結果出力
'   ↓
'ブートストラップ関係

'ここから下は全てサブルーチン

DataSet:
Worksheets("data input").Activate

    'VPA 用の F の初期値
    For CdataNum = 1 To CatchNum
        For Ag = 1 To AgeNum
            For Yr = 1 To AgeNum
                F(Ag, YrNum - Yr) = 0.5
                Feach(Ag, YrNum - Yr, CdataNum) = 0.5
            Next Yr
        Next Ag
    Next CdataNum

'*************************
'*                       *
'*       DATA INPUT      *
'*                       *
'*************************
    M = ActiveSheet.Cells(4, 6)

    For Yr = 1 To YrNum
        For Ag = 1 To AgeNum
            Csum(Ag, Yr) = 0
        Next Ag
    Next Yr

    RecruitmentAge = ActiveSheet.Cells(6, 2)
    StartYear = ActiveSheet.Cells(4, 2)
```

```
    For CdataNum = 1 To CatchNum
        For Yr = 1 To YrNum
            For Ag = 1 To AgeNum
            C(Ag, Yr, CdataNum) = ActiveSheet.Cells(10 + (AgeNum + 3 + 1) * CdataNum + Ag, Yr + 1)
            Csum(Ag, Yr) = Csum(Ag, Yr) + C(Ag, Yr, CdataNum) 'Catch Sum
            aveW(Ag) = ActiveSheet.Cells(10 + Ag, 6)
            aveW(Ag) = aveW(Ag) / 1000000      '平均体重(g→t)
            Next Ag
        Next Yr
    Next CdataNum

    For CdataNum = 1 To qNum
        For Yr = 1 To YrNum
            LnCPUE(Yr, CdataNum) = ActiveSheet.Cells(10 + (AgeNum + 3 + 1) * CdataNum + AgeNum + 1, Yr
            + 1)
            If CPUEweight = 2 Then CPUEcv(Yr, CdataNum) = ActiveSheet.Cells(10 + (AgeNum + 3 + 1) *
            CdataNum + AgeNum + 2, Yr + 1)
        Next Yr
    Next CdataNum

'*********************************
'*                               *
'*      パラメータ初期値入力     *
'*                               *
'*********************************
    F(AgeNum, YrNum) = ActiveSheet.Cells(11, 3)
    For CdataNum = 1 To qNum
        'q data input
        q(CdataNum) = ActiveSheet.Cells(11 + CdataNum, 3)
    Next CdataNum

Worksheets("calculation").Activate
    ActiveSheet.Cells(8, 1) = "SSQ"

    'F を Simplex 用の変数に変換
        x(1, 1) = F(AgeNum, YrNum)

    'q を Simplex 用の変数に変換
        For CdataNum = 1 To qNum
        x(1, 1 + CdataNum) = q(CdataNum)
    Next CdataNum
Return


'*****************************
'*                           *
'*       Simplex START       *
'*                           *
'*****************************
Simplex:
Worksheets("calculation").Activate
    fBefore = 1000
    ActiveSheet.Cells(7, 1) = "Repeat: " & bt

retry:
    For i = 2 To paraNum + 1
        For j = 1 To paraNum
            x(i, j) = x(1, j) * (1 + (Rnd - 0.5) * 0.05)       'Simplex のデータセット作成
            ActiveSheet.Cells(11, 1 + j) = x(1, j)
```

```
            ActiveSheet.Cells(10 + i, 1 + j) = x(i, j)
        Next j
    Next i

    For k = 1 To paraNum + 1
        For Ag = 1 To paraNum
            x(k, Ag) = Log(x(k, Ag))
        Next Ag
    Next k

    For k = 1 To paraNum + 1
        For i = 1 To paraNum
            paraMeter(i) = x(k, i)
        Next i
    GoSub VPA1

    ActiveSheet.Cells(10 + k, 1) = ssq
        Fssq(k) = ssq
    Next k

    For i = 1 To paraNum
        For j = i + 1 To paraNum + 1

            If Fssq(i) < Fssq(j) Then
                d = Fssq(i)
                Fssq(i) = Fssq(j)
                Fssq(j) = d

            For L = 1 To paraNum
                d = x(i, L)
                x(i, L) = x(j, L)
                x(j, L) = d
            Next L
            End If
        Next j
    Next i

    fHigh = Fssq(1): fSecond = Fssq(2): fSmall = Fssq(paraNum + 1)
    For i = 1 To paraNum
        Xhigh(i) = x(1, i): xSecond(i) = x(2, i): Xsmall(i) = x(paraNum + 1, i)
    Next i

    For i = 1 To paraNum
        For j = 2 To paraNum + 1
            x0(i) = x0(i) + x(j, i)
        Next j
    Next i

    aa = 1

    Do Until aa < 0.00000000001
    fr = 0: fc = 0: fe = 0
    For i = 1 To paraNum
        xr(i) = 0: xe(i) = 0: xc(i) = 0
    Next i

    For i = 1 To paraNum
        xr(i) = 2 / (paraNum) * x0(i) - Xhigh(i)
        paraMeter(i) = xr(i)
```

```
Next i
GoSub VPA1

fr = ssq

Select Case fr
Case Is <= fSecond

    If fr >= fSmall Then
        Fssq(1) = fr
        For i = 1 To paraNum
            x(1, i) = xr(i)
        Next i
    ElseIf fr < fSmall Then

        For i = 1 To paraNum
            xe(i) = 2 * xr(i) - x0(i) / (paraNum)
            paraMeter(i) = xe(i)
        Next i
    GoSub VPA1
            fe = ssq
        End If

    If fr >= fSmall Then
        Fssq(1) = fr
        For i = 1 To paraNum
            x(1, i) = xr(i)
        Next i
    ElseIf fe >= fr Then
        Fssq(1) = fr
        For i = 1 To paraNum
            x(1, i) = xr(i)
        Next i
    ElseIf fe < fr Then
        Fssq(1) = fe
        For i = 1 To paraNum
            x(1, i) = xe(i)
        Next i
    End If

Case Is > fSecond

    If fr < fHigh Then
        For i = 1 To paraNum
            Xhigh(i) = xr(i)
        Next i
    End If

    For i = 1 To paraNum
        xc(i) = 0.5 * Xhigh(i) + 0.5 / (paraNum) * x0(i)
            paraMeter(i) = xc(i)
        Next i
    GoSub VPA1

    fc = ssq

    If fc < fHigh Then
    Fssq(1) = fc
        For i = 1 To paraNum
```

```
            x(1, i) = xc(i)
        Next i

ElseIf fc >= fHigh Then
    For i = 1 To paraNum + 1
        For j = 1 To paraNum
            x(i, j) = 1 / 2 * (x(i, j) + Xsmall(j))
        Next j
    Next i

    For k = 1 To paraNum + 1
        For i = 1 To paraNum
            paraMeter(i) = x(k, i)
        Next i
    GoSub VPA1

    Fssq(k) = ssq
    Next k

End If
End Select

    For i = 1 To paraNum
        For j = i + 1 To paraNum + 1
        If Fssq(i) < Fssq(j) Then
        d = Fssq(i)
        Fssq(i) = Fssq(j)
        Fssq(j) = d

        For L = 1 To paraNum
            d = x(i, L)
            x(i, L) = x(j, L)
            x(j, L) = d
        Next L
End If
        Next j
    Next i

fHigh = Fssq(1): fSecond = Fssq(2): fSmall = Fssq(paraNum + 1)
For i = 1 To paraNum
    Xhigh(i) = x(1, i): xSecond(i) = x(2, i): Xsmall(i) = x(paraNum + 1, i)
Next i

For i = 1 To paraNum
    x0(i) = 0
    For j = 2 To paraNum + 1
        x0(i) = x0(i) + x(j, i)
    Next j
Next i

aa = 0
fAve1 = 0
fAve2 = 0
For i = 1 To paraNum + 1
    fAve1 = fAve1 + Fssq(i)
Next i
fAve1 = 1 / (paraNum + 1) * fAve1
For i = 1 To paraNum + 1
    fAve2 = fAve2 + (Fssq(i) - fAve1) ^ 2
```

```
    Next i
    aa = (1 / (paraNum + 1) * fAve2) ^ 0.5

    ActiveSheet.Cells(9, 1) = ssq

    Loop
    For i = 1 To paraNum + 1
        For j = 1 To paraNum
            ActiveSheet.Cells(10 + i, 1) = Fssq(i)
            ActiveSheet.Cells(10 + i, 1 + j) = Exp(x(i, j))
        Next j
    Next i
    If fBefore > fHigh + 0.000000001 Then
    fBefore = fHigh
        For i = 1 To paraNum
            x(1, i) = Exp(x(1, i))
        Next i

    GoTo retry:
    End If

    For i = 1 To paraNum
        x(1, i) = Exp(x(1, i))
    Next i
Return


'*************************
'*                       *
'*    VPA Sub Routine    *最高齢のFは最高齢－1歳のFのα倍
'*                       *
'*************************
VPA_Fmax_age_const:
    ssq = 0

    For CdataNum = 1 To CatchNum
        For Yr = 1 To YrNum
            SN(Yr, CdataNum) = 0
        Next Yr
    Next CdataNum
    'Simplex のパラメータ q を目的関数のパラメータ名に変換

    For CdataNum = 1 To qNum
        q(CdataNum) = Exp(paraMeter(1 + CdataNum))
    Next CdataNum

    '最近年のFの仮定
    'Simplex のパラメータFを目的関数のパラメータ名に変換
    paraAg = 4      '最近年何歳が未知パラメータか指定
        F(paraAg, YrNum) = Exp(paraMeter(1))

    If selectivityPattern = 2 Then GoTo sepa2
    '全体の選択率から最近年推定
    For Ag = 1 To 4
    Select Case backYr
    Case Is = 1     '前年の比と同じ
        F(Ag, YrNum) = (F(Ag, YrNum - 1)) / (F(paraAg, YrNum - 1)) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-1-1"
    Case Is = 2     '過去2年の比と同じ
```

```
        F(Ag, YrNum) = (F(Ag, YrNum - 1) + F(Ag, YrNum - 2)) / (F(paraAg, YrNum - 1) + F(paraAg, YrNum -
        2)) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-1-2"
    Case Is = 3      '過去 3 年の比と同じ
        F(Ag, YrNum) = (F(Ag, YrNum - 1) + F(Ag, YrNum - 2) + F(Ag, YrNum - 3)) / (F(paraAg, YrNum - 1) +
        F(paraAg, YrNum - 2) + F(paraAg, YrNum - 3)) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-1-3"
    Case Is = 4      '過去 4 年の比と同じ
        F(Ag, YrNum) = (F(Ag, YrNum - 1) + F(Ag, YrNum - 2) + F(Ag, YrNum - 3) + F(Ag, YrNum - 4)) /
        (F(paraAg, YrNum - 1) + F(paraAg, YrNum - 2) + F(paraAg, YrNum - 3) + F(paraAg, YrNum - 4)) *
        F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-1-4"
    Case Is = 5      '過去 5 年の比と同じ
        F(Ag, YrNum) = (F(Ag, YrNum - 1) + F(Ag, YrNum - 2) + F(Ag, YrNum - 3) + F(Ag, YrNum - 4) + F(Ag,
        YrNum - 5)) / (F(paraAg, YrNum - 1) + F(paraAg, YrNum - 2) + F(paraAg, YrNum - 3) + F(paraAg,
        YrNum - 4) + F(paraAg, YrNum - 5)) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-1-5"
    End Select

    Next Ag
    GoTo sepa1

sepa2:
    '各漁業の選択率から最近年推定
    For Ag = 1 To 4
        For CdataNum = 1 To CatchNum
    Select Case backYr
    Case Is = 1      '前年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum)) / (Feach(paraAg, YrNum - 1, CdataNum)) * C(Ag,
        YrNum, CdataNum) / Csum(Ag, YrNum) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-2-1"
    Case Is = 2      '過去 2 年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum) + Feach(Ag, YrNum - 2, CdataNum)) / (Feach(paraAg,
        YrNum - 1, CdataNum) + Feach(paraAg, YrNum - 2, CdataNum)) * C(Ag, YrNum, CdataNum) / Csum(Ag,
        YrNum) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-2-2"
    Case Is = 3      '過去 3 年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum) + Feach(Ag, YrNum - 2, CdataNum) + Feach(Ag, YrNum
        - 3, CdataNum)) / (Feach(paraAg, YrNum - 1, CdataNum) + Feach(paraAg, YrNum - 2, CdataNum) +
        Feach(paraAg, YrNum - 3, CdataNum)) * C(Ag, YrNum, CdataNum) / Csum(Ag, YrNum) * F(paraAg,
        YrNum)
        ActiveSheet.Cells(1, 1) = "2-2-3"
    Case Is = 4      '過去 4 年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum) + Feach(Ag, YrNum - 2, CdataNum) + Feach(Ag, YrNum
        - 3, CdataNum) + Feach(Ag, YrNum - 4, CdataNum)) / (Feach(paraAg, YrNum - 1, CdataNum) +
        Feach(paraAg, YrNum - 2, CdataNum) + Feach(paraAg, YrNum - 3, CdataNum) + Feach(paraAg, YrNum
        - 4, CdataNum)) * C(Ag, YrNum, CdataNum) / Csum(Ag, YrNum) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-2-4"
    Case Is = 5      '過去 5 年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum) + Feach(Ag, YrNum - 2, CdataNum) + Feach(Ag, YrNum
        - 3, CdataNum) + Feach(Ag, YrNum - 4, CdataNum) + Feach(Ag, YrNum - 5, CdataNum)) /
        (Feach(paraAg, YrNum - 1, CdataNum) + Feach(paraAg, YrNum - 2, CdataNum) + Feach(paraAg, YrNum
        - 3, CdataNum) + Feach(paraAg, YrNum - 4, CdataNum) + Feach(paraAg, YrNum - 5, CdataNum)) *
        C(Ag, YrNum, CdataNum) / Csum(Ag, YrNum) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "2-2-5"
    End Select
        Next CdataNum
            F(Ag, YrNum) = Fay
            Fay = 0
```

```
    Next Ag

sepa1:
    '最高年齢の F(ターミナル F)の仮定　Ftmax=alpha*Ftmax-1
    F(AgeNum, YrNum) = alpha * F(AgeNum - 1, YrNum)

    For Ag = 1 To AgeNum
        Fans(Ag, YrNum) = F(Ag, YrNum)
    Next Ag

    Select Case alpha
    Case Is = 1 '最高齢の資源尾数計算 alpha=1 のとき

    For Yr = YrNum To 2 Step -1
    N(AgeNum, Yr) = Csum(AgeNum, Yr) / (F(AgeNum, Yr) / (F(AgeNum, Yr) + M) * (1 - Exp(-F(AgeNum, Yr) -
    M)))
        Do
            Fa(AgeNum, Yr) = F(AgeNum, Yr)
            Fb(AgeNum - 1, Yr - 1) = F(AgeNum, Yr) - (Csum(AgeNum, Yr - 1) + Csum(AgeNum - 1, Yr - 1) -
            N(AgeNum, Yr) * F(AgeNum, Yr) / (F(AgeNum, Yr) + M) * (1 - Exp(-F(AgeNum, Yr) - M)) *
            (Exp(F(AgeNum, Yr) + M))) / ((-N(AgeNum, Yr) * M * Exp(F(AgeNum, Yr) + M) + (N(AgeNum, Yr) *
            M) - N(AgeNum, Yr) * F(AgeNum, Yr) * (F(AgeNum, Yr) + M) * Exp(F(AgeNum, Yr) + M)) /
            (F(AgeNum, Yr) + M) ^ 2)
            F(AgeNum, Yr) = Fb(AgeNum - 1, Yr - 1)
        Loop Until (Fa(AgeNum, Yr) / Fb(AgeNum - 1, Yr - 1) - 1) ^ 2 <= 0.00000000000001
            F(AgeNum - 1, Yr - 1) = Fb(AgeNum - 1, Yr - 1)
            F(AgeNum, Yr - 1) = Fb(AgeNum - 1, Yr - 1)
            Fans(AgeNum - 1, Yr - 1) = Fb(AgeNum - 1, Yr - 1)
            Fans(AgeNum, Yr - 1) = Fb(AgeNum - 1, Yr - 1)
    Next Yr

    Case Else '最高齢の資源尾数計算 alpha1 以外のとき
    ActiveSheet.Cells(5, 2) = "alpha1 以外"
    For Yr = YrNum To 2 Step -1
    N(AgeNum, Yr) = Csum(AgeNum, Yr) / (F(AgeNum, Yr) / (F(AgeNum, Yr) + M) * (1 - Exp(-F(AgeNum, Yr) -
    M)))
        Do
            Fa(AgeNum, Yr) = F(AgeNum, Yr)
            sa = sa + 1
            Fb(AgeNum - 1, Yr - 1) = F(AgeNum, Yr) - (Csum(AgeNum - 1, Yr - 1) * (F(AgeNum, Yr) + M) /
            F(AgeNum, Yr) * Exp(-F(AgeNum, Yr) - M) / (1 - Exp(-F(AgeNum, Yr) - M)) + Csum(AgeNum, Yr -
            1) * (alpha * F(AgeNum, Yr) + M) / (alpha * F(AgeNum, Yr)) * Exp(-alpha * F(AgeNum, Yr) - M) /
            (1 - Exp(-alpha * F(AgeNum, Yr) - M)) - N(AgeNum, Yr)) / (Csum(AgeNum - 1, Yr - 1) * (-M /
            (F(AgeNum, Yr) * F(AgeNum, Yr)) * Exp(-F(AgeNum, Yr) - M) / (1 - Exp(-F(AgeNum, Yr) - M)) +
            (F(AgeNum, Yr) + M) / F(AgeNum, Yr) * (-Exp(-F(AgeNum, Yr) - M)) / ((1 - Exp(-F(AgeNum, Yr) -
            M)) ^ 2)) + Csum(AgeNum, Yr - 1) * (-M / (alpha * F(AgeNum, Yr) ^ 2) * Exp(-alpha * F(AgeNum,
            Yr) - M) / (1 - Exp(-alpha * F(AgeNum, Yr) - M)) + (alpha * F(AgeNum, Yr) + M) / (alpha *
            F(AgeNum, Yr)) * (-alpha * Exp(-alpha * F(AgeNum, Yr) - M)) / ((1 - Exp(-alpha * F(AgeNum, Yr)
            - M)) ^ 2)))
            F(AgeNum, Yr) = Fb(AgeNum - 1, Yr - 1)
        Loop Until (Fa(AgeNum, Yr) / Fb(AgeNum - 1, Yr - 1) - 1) ^ 2 <= 0.00000000000001
            F(AgeNum, Yr - 1) = alpha * Fb(AgeNum - 1, Yr - 1)
            F(AgeNum - 1, Yr - 1) = Fb(AgeNum - 1, Yr - 1)
            Fans(AgeNum, Yr - 1) = alpha * Fb(AgeNum - 1, Yr - 1)
            Fans(AgeNum - 1, Yr - 1) = Fb(AgeNum - 1, Yr - 1)
    Next Yr
    End Select

    '最高齢-1 歳から加入の翌年までの資源尾数計算
```

```
    For Yr = YrNum To 2 Step -1
    For Ag = AgeNum - 1 To 2 Step -1
    If Csum(Ag, Yr) > 0 Then N(Ag, Yr) = Csum(Ag, Yr) / (F(Ag, Yr) / (F(Ag, Yr) + M) * (1 - Exp(-F(Ag, Yr) - M)))
    Else N(Ag, Yr) = N(Ag + 1, Yr + 1) * Exp(M)
    If Csum(Ag - 1, Yr - 1) = 0 Then GoTo 1000:
        Do
            Fa(Ag, Yr) = F(Ag, Yr)
            Fb(Ag - 1, Yr - 1) = F(Ag, Yr) - (Csum(Ag - 1, Yr - 1) - N(Ag, Yr) * F(Ag, Yr) / (F(Ag, Yr) + M) * (1
            - Exp(-F(Ag, Yr) - M)) * (Exp(F(Ag, Yr) + M))) / ((-N(Ag, Yr) * M * Exp(F(Ag, Yr) + M) + (N(Ag, Yr)
            * M) - N(Ag, Yr) * F(Ag, Yr) * (F(Ag, Yr) + M) * Exp(F(Ag, Yr) + M)) / (F(Ag, Yr) + M) ^ 2)
            F(Ag, Yr) = Fb(Ag - 1, Yr - 1)
        Loop Until (Fa(Ag, Yr) / Fb(Ag - 1, Yr - 1) - 1) ^ 2 <= 0.00000000000001
            F(Ag - 1, Yr - 1) = Fb(Ag - 1, Yr - 1)
            Fans(Ag - 1, Yr - 1) = Fb(Ag - 1, Yr - 1)
        GoTo 1100:
1000:
        F(Ag - 1, Yr - 1) = 0
        Fans(Ag - 1, Yr - 1) = 0
1100:
        Next Ag
    Next Yr

    For Yr = YrNum To 1 Step -1
        If Csum(1, Yr) = 0 Then GoTo 2000:
        N(1, Yr) = Csum(1, Yr) / (Fans(1, Yr) / (Fans(1, Yr) + M) * (1 - Exp(-Fans(1, Yr) - M)))
    GoTo 2100:
2000:
    N(1, Yr) = N(2, Yr + 1) * Exp(M)
2100:
    Next Yr

    For Ag = AgeNum To 1 Step -1
        If Csum(Ag, 1) = 0 Then GoTo 3000:
        N(Ag, 1) = Csum(Ag, 1) / (Fans(Ag, 1) / (Fans(Ag, 1) + M) * (1 - Exp(-Fans(Ag, 1) - M)))
    GoTo 3100:
3000:
    N(Ag, 1) = N(Ag + 1, 2) * Exp(M)
3100:
    Next Ag

    '***選択率計算

    For CdataNum = 1 To CatchNum
        '漁法別Fの推定
        For Ag = 1 To AgeNum
            For Yr = 1 To YrNum
                If Csum(Ag, Yr) = 0 Then GoTo 4000:
                Feach(Ag, Yr, CdataNum) = C(Ag, Yr, CdataNum) / Csum(Ag, Yr) * Fans(Ag, Yr)
    GoTo 4100:
4000:
        Feach(Ag, Yr, CdataNum) = 0
4100:
            Next Yr
        Next Ag
    Next CdataNum

    'ある年のFの最大値
    For CdataNum = 1 To CatchNum
        For Yr = 1 To YrNum
```

```
            FaMax(Yr, CdataNum) = Feach(1, Yr, CdataNum)
            For Ag = 2 To AgeNum
                If FaMax(Yr, CdataNum) < Feach(Ag, Yr, CdataNum) Then
                FaMax(Yr, CdataNum) = Feach(Ag, Yr, CdataNum)
                End If
            Next Ag
        Next Yr
    Next CdataNum

    '選択率計算
    For CdataNum = 1 To qNum
        For Ag = 1 To AgeNum
            For Yr = 1 To YrNum
                S(Ag, Yr, CdataNum) = Feach(Ag, Yr, CdataNum) / FaMax(Yr, CdataNum)
            Next Yr
        Next Ag
    Next CdataNum

    '平均資源量の計算
    For Yr = 1 To YrNum
        For Ag = 1 To AgeNum
            Nave(Ag, Yr) = N(Ag, Yr) / (Fans(Ag, Yr) + M) * (1 - Exp(-Fans(Ag, Yr) - M))
        Next Ag
    Next Yr

    For CdataNum = 1 To CatchNum
        For Yr = 1 To YrNum
            For Ag = 1 To AgeNum
                SN(Yr, CdataNum) = SN(Yr, CdataNum) + Nave(Ag, Yr) * S(Ag, Yr, CdataNum)
            Next Ag
        Next Yr
    Next CdataNum

    For CdataNum = 1 To qNum
        For Yr = 1 To YrNum
            If CPUEweight = 1 Then ssq = ssq + ((LnCPUE(Yr, CdataNum)) - Log(q(CdataNum) * SN(Yr,
            CdataNum))) ^ 2
            If CPUEweight = 2 Then ssq = ssq + ((LnCPUE(Yr, CdataNum)) - Log(q(CdataNum) * SN(Yr,
        CdataNum))) ^ 2 / CPUEcv(Yr, CdataNum)
        Next Yr
    Next CdataNum

    For Ag = 1 To 4
        For Yr = 1 To 4
            F(Ag, YrNum - Yr) = Fans(Ag, YrNum - Yr)
        Next Yr
    Next Ag
Return


'************************
'*                      *
'*    VPA Sub Routine    *最高齢のＦは一定と仮定
'*                      *
'************************
VPA_Fmax_year_const:
    ssq = 0

    For CdataNum = 1 To CatchNum
```

```
        For Yr = 1 To YrNum
            SN(Yr, CdataNum) = 0
        Next Yr
    Next CdataNum
    'Simplex のパラメータ q を目的関数のパラメータ名に変換

    For CdataNum = 1 To qNum
        q(CdataNum) = Exp(paraMeter(1 + CdataNum))
    Next CdataNum

    '最近年の F の仮定
    'Simplex のパラメータ F を目的関数のパラメータ名に変換

    paraAg = AgeNum '最近年何歳が未知パラメータか指定
        F(AgeNum, YrNum) = Exp(paraMeter(1))
        Fans(AgeNum, YrNum) = Exp(paraMeter(1))

    If selectivityPattern = 2 Then GoTo sepa02
    '全体の選択率から最近年推定
    For Ag = 1 To AgeNum - 1
    Select Case backYr
    Case Is = 1      '前年の比と同じ
        F(Ag, YrNum) = (F(Ag, YrNum - 1)) / (F(paraAg, YrNum - 1)) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "1-1-1"
    Case Is = 2      '過去 2 年の比と同じ
        F(Ag, YrNum) = (F(Ag, YrNum - 1) + F(Ag, YrNum - 2)) / (F(paraAg, YrNum - 1) + F(paraAg, YrNum -
        2)) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "1-1-2"
    Case Is = 3      '過去 3 年の比と同じ
        F(Ag, YrNum) = (F(Ag, YrNum - 1) + F(Ag, YrNum - 2) + F(Ag, YrNum - 3)) / (F(paraAg, YrNum - 1) +
        F(paraAg, YrNum - 2) + F(paraAg, YrNum - 3)) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "1-1-3"
    Case Is = 4      '過去 4 年の比と同じ
        F(Ag, YrNum) = (F(Ag, YrNum - 1) + F(Ag, YrNum - 2) + F(Ag, YrNum - 3) + F(Ag, YrNum - 4)) /
        (F(paraAg, YrNum - 1) + F(paraAg, YrNum - 2) + F(paraAg, YrNum - 3) + F(paraAg, YrNum - 4)) *
        F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "1-1-4"

    End Select
    Next Ag
    GoTo sepa01

sepa02:
    '各漁業の選択率から最近年推定
    For Ag = 1 To AgeNum - 1
        For CdataNum = 1 To CatchNum
    Select Case backYr
    Case Is = 1      '前年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum)) / (Feach(paraAg, YrNum - 1, CdataNum)) * C(Ag,
        YrNum, CdataNum) / Csum(Ag, YrNum) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "1-2-1"
    Case Is = 2      '過去 2 年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum) + Feach(Ag, YrNum - 2, CdataNum))/ (Feach(paraAg,
        YrNum - 1, CdataNum) + Feach(paraAg, YrNum - 2, CdataNum)) * C(Ag, YrNum, CdataNum) / Csum(Ag,
        YrNum) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "1-2-2"
    Case Is = 3      '過去 3 年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum) + Feach(Ag, YrNum - 2, CdataNum) + Feach(Ag, YrNum
        - 3, CdataNum)) / (Feach(paraAg, YrNum - 1, CdataNum) + Feach(paraAg, YrNum - 2, CdataNum) +
```

```
        Feach(paraAg, YrNum - 3, CdataNum)) * C(Ag, YrNum, CdataNum) / Csum(Ag, YrNum) * F(paraAg,
        YrNum)
        ActiveSheet.Cells(1, 1) = "1-2-3"
    Case Is = 4      '過去 4 年の比と同じ
        Fay = Fay + (Feach(Ag, YrNum - 1, CdataNum) + Feach(Ag, YrNum - 2, CdataNum) + Feach(Ag, YrNum
        - 3, CdataNum) + Feach(Ag, YrNum - 4, CdataNum)) / (Feach(paraAg, YrNum - 1, CdataNum) +
        Feach(paraAg, YrNum - 2, CdataNum) + Feach(paraAg, YrNum - 3, CdataNum) + Feach(paraAg, YrNum
        - 4, CdataNum)) * C(Ag, YrNum, CdataNum) / Csum(Ag, YrNum) * F(paraAg, YrNum)
        ActiveSheet.Cells(1, 1) = "1-2-4"

    End Select
        Next CdataNum
        F(Ag, YrNum) = Fay
        Fay = 0
    Next Ag
sepa01:

    '最高年齢の F(ターミナル F)の仮定　Fa+=一定
    For Yr = 1 To YrNum
        F(AgeNum, Yr) = F(AgeNum, YrNum)
        Fans(AgeNum, Yr) = F(AgeNum, YrNum)
    Next Yr

    For Ag = 1 To AgeNum
        Fans(Ag, YrNum) = F(Ag, YrNum)
    Next Ag

    '最高齢の資源尾数計算
    For Yr = YrNum To 2 Step -1
        N(AgeNum, Yr) = Csum(AgeNum, Yr) / (F(AgeNum, Yr) / (F(AgeNum, Yr) + M) * (1 - Exp(-F(AgeNum,
        Yr) - M)))
        Na(AgeNum, Yr) = N(AgeNum, Yr) - Csum(AgeNum, Yr - 1) / (F(AgeNum, Yr - 1) / (F(AgeNum, Yr - 1)
        + M) * (1 - Exp(-F(AgeNum, Yr - 1) - M))) * Exp(-F(AgeNum, Yr - 1) - M)
        Do
            Fa(AgeNum, Yr) = F(AgeNum, Yr)
            Fb(AgeNum - 1, Yr - 1) = F(AgeNum, Yr) - (Csum(AgeNum - 1, Yr - 1) - Na(AgeNum, Yr) *
            F(AgeNum, Yr) / (F(AgeNum, Yr) + M) * (1 - Exp(-F(AgeNum, Yr) - M)) * (Exp(F(AgeNum, Yr) + M)))
            / ((-N(AgeNum, Yr) * M * Exp(F(AgeNum, Yr) + M) + (Na(AgeNum, Yr) * M) - N(AgeNum, Yr) *
            F(AgeNum, Yr) * (F(AgeNum, Yr) + M) * Exp(F(AgeNum, Yr) + M)) / (F(AgeNum, Yr) + M) ^ 2)
            F(AgeNum, Yr) = Fb(AgeNum - 1, Yr - 1)
        Loop Until (Fa(AgeNum, Yr) / Fb(AgeNum - 1, Yr - 1) - 1) ^ 2 <= 0.00000000000001

        F(AgeNum, Yr) = Fans(AgeNum, Yr)

        F(AgeNum - 1, Yr - 1) = Fb(AgeNum - 1, Yr - 1)
        Fans(AgeNum - 1, Yr - 1) = Fb(AgeNum - 1, Yr - 1)
    Next Yr

    '最高齢-1 歳から加入の翌年までの資源尾数計算
    For Yr = YrNum To 2 Step -1
        For Ag = AgeNum - 1 To 2 Step -1
            If Csum(Ag, Yr) > 0 Then N(Ag, Yr) = Csum(Ag, Yr) / (F(Ag, Yr) / (F(Ag, Yr) + M) * (1 - Exp(-F(Ag,
            Yr) - M))) Else N(Ag, Yr) = N(Ag + 1, Yr + 1) * Exp(M)
            If Csum(Ag - 1, Yr - 1) = 0 Then GoTo 11000:
            Do
            Fa(Ag, Yr) = F(Ag, Yr)
            Fb(Ag - 1, Yr - 1) = F(Ag, Yr) - (Csum(Ag - 1, Yr - 1) - N(Ag, Yr) * F(Ag, Yr) / (F(Ag, Yr) + M) * (1
            - Exp(-F(Ag, Yr) - M)) * (Exp(F(Ag, Yr) + M))) / ((-N(Ag, Yr) * M * Exp(F(Ag, Yr) + M) + (N(Ag, Yr)
            * M) - N(Ag, Yr) * F(Ag, Yr) * (F(Ag, Yr) + M) * Exp(F(Ag, Yr) + M)) / (F(Ag, Yr) + M) ^ 2)
```

```
            F(Ag, Yr) = Fb(Ag - 1, Yr - 1)
            Loop Until (Fa(Ag, Yr) / Fb(Ag - 1, Yr - 1) - 1) ^ 2 <= 0.00000000000001
            F(Ag - 1, Yr - 1) = Fb(Ag - 1, Yr - 1)
            Fans(Ag - 1, Yr - 1) = Fb(Ag - 1, Yr - 1)
            GoTo 11100:
11000:
        F(Ag - 1, Yr - 1) = 0
        Fans(Ag - 1, Yr - 1) = 0
11100:
        Next Ag
    Next Yr

    For Yr = YrNum To 1 Step -1
        If Csum(1, Yr) = 0 Then GoTo 12000:
        N(1, Yr) = Csum(1, Yr) / (Fans(1, Yr) / (Fans(1, Yr) + M) * (1 - Exp(-Fans(1, Yr) - M)))
        GoTo 12100:
12000:
        N(1, Yr) = N(2, Yr + 1) * Exp(M)
12100:
    Next Yr

    For Ag = AgeNum To 1 Step -1
        If Csum(Ag, 1) = 0 Then GoTo 13000:
            N(Ag, 1) = Csum(Ag, 1) / (Fans(Ag, 1) / (Fans(Ag, 1) + M) * (1 - Exp(-Fans(Ag, 1) - M)))
    GoTo 13100:
13000:
    N(Ag, 1) = N(Ag + 1, 2) * Exp(M)
13100:
    Next Ag

    For CdataNum = 1 To CatchNum
    '漁法別 F の推定
        For Ag = 1 To AgeNum
            For Yr = 1 To YrNum
            If Csum(Ag, Yr) = 0 Then GoTo 14000:
            Feach(Ag, Yr, CdataNum) = C(Ag, Yr, CdataNum) / Csum(Ag, Yr) * Fans(Ag, Yr)
            GoTo 14100:
14000:
            Feach(Ag, Yr, CdataNum) = 0
14100:
            Next Yr
        Next Ag
    Next CdataNum

    'ある年の F の最大値
    For CdataNum = 1 To CatchNum
        For Yr = 1 To YrNum
            FaMax(Yr, CdataNum) = Feach(1, Yr, CdataNum)
            For Ag = 2 To AgeNum
                If FaMax(Yr, CdataNum) < Feach(Ag, Yr, CdataNum) Then
                FaMax(Yr, CdataNum) = Feach(Ag, Yr, CdataNum)
                End If
            Next Ag
        Next Yr
    Next CdataNum

    '選択率計算
    For CdataNum = 1 To qNum
        For Ag = 1 To AgeNum
```

```
            For Yr = 1 To YrNum
                S(Ag, Yr, CdataNum) = Feach(Ag, Yr, CdataNum) / FaMax(Yr, CdataNum)
            Next Yr
        Next Ag
    Next CdataNum

    '平均資源量の計算
        For Yr = 1 To YrNum
            For Ag = 1 To AgeNum
                Nave(Ag, Yr) = N(Ag, Yr) / (Fans(Ag, Yr) + M) * (1 - Exp(-Fans(Ag, Yr) - M))
            Next Ag
        Next Yr

    For CdataNum = 1 To CatchNum
        For Yr = 1 To YrNum
            For Ag = 1 To AgeNum
                SN(Yr, CdataNum) = SN(Yr, CdataNum) + Nave(Ag, Yr) * S(Ag, Yr, CdataNum)
            Next Ag
        Next Yr
    Next CdataNum

    For CdataNum = 1 To qNum
        For Yr = 1 To YrNum
            If CPUEweight = 1 Then ssq = ssq + ((LnCPUE(Yr, CdataNum)) - Log(q(CdataNum) * SN(Yr,
            CdataNum))) ^ 2
            If CPUEweight = 2 Then ssq = ssq + ((LnCPUE(Yr, CdataNum)) - Log(q(CdataNum) * SN(Yr,
            CdataNum))) ^ 2 / CPUEcv(Yr, CdataNum)
        Next Yr
    Next CdataNum

    For Ag = 1 To 4
        For Yr = 1 To 4
            F(Ag, YrNum - Yr) = Fans(Ag, YrNum - Yr)
        Next Yr
    Next Ag
Return


OutPut:
Worksheets("VPA").Activate
'************************
'*                      *
'*    Frame & OutPut    *
'*                      *
'************************

    For CdataNum = 1 To CatchNum

        ActiveSheet.Cells(10, 1) = "N(尾数)"
        ActiveSheet.Cells(10 + AgeNum + 2, 1) = "N(重量)(t)"
        ActiveSheet.Cells(10 + 7 + AgeNum * 2, 1) = "F total"
        ActiveSheet.Cells(10 + (7 + AgeNum * 2) * (1 + CdataNum), 1) = "F-" & CdataNum

        For Ag = 1 To AgeNum
            ActiveSheet.Cells(10 + Ag, 1) = RecruitmentAge + Ag - 1      'N の年齢の行出力(尾数)
            ActiveSheet.Cells(10 + AgeNum + 2 + Ag, 1) = RecruitmentAge + Ag - 1        'N の年齢の行出力
            (重量)
            ActiveSheet.Cells(10 + 7 + AgeNum * 2 + Ag, 1) = RecruitmentAge + Ag - 1        '全体の F の行
            出力(年齢)
```

```
        '全体のFの行出力(年齢)
        ActiveSheet.Cells(10 + (7 + AgeNum * 2) * (CdataNum + 1) + Ag, 1) = RecruitmentAge + Ag - 1
    Next Ag

    For Yr = 1 To YrNum
        ActiveSheet.Cells(10, 1 + Yr) = StartYear + Yr - 1          'Nの年の列出力(尾数)
        ActiveSheet.Cells(10 + AgeNum + 2, 1 + Yr) = StartYear + Yr - 1      'Nの年の列出力(重量)
        ActiveSheet.Cells(10 + 7 + AgeNum * 2, 1 + Yr) = StartYear + Yr - 1        '全体の F の列出力
        (年)
        '各漁業のFの列出力(年)
        ActiveSheet.Cells(10 + (7 + AgeNum * 2) * (CdataNum + 1), 1 + Yr) = StartYear + Yr - 1
    Next Yr
    ActiveSheet.Cells(10, 1 + YrNum + 1) = StartYear + YrNum   '翌年のNの年表示(尾数)
    ActiveSheet.Cells(10 + AgeNum + 2, 1 + YrNum + 1) = StartYear + YrNum     '翌年のNの年表示(重
    量)

    For Ag = 1 To AgeNum
        For Yr = 1 To YrNum
        ActiveSheet.Cells(10 + Ag, 1 + Yr) = N(Ag, Yr) 'Nの出力(尾数)
        ActiveSheet.Cells(10 + AgeNum + 2 + Ag, 1 + Yr) = N(Ag, Yr) * aveW(Ag)       'Nの出力(重量(t))
        '全体のFの出力
        ActiveSheet.Cells(10 + 7 + AgeNum * 2 + Ag, 1 + Yr) = Fans(Ag, Yr)       '各漁業のFの出力
        ActiveSheet.Cells(10 + (7 + AgeNum * 2) * (CdataNum + 1) + Ag, 1 + Yr) = Feach(Ag, Yr,
        CdataNum)
        Next Yr
    Next Ag
Next CdataNum

'翌年の加入尾数
For Ag = 2 To AgeNum - 1
    ActiveSheet.Cells(10 + Ag, 1 + YrNum + 1) = N(Ag - 1, YrNum) * Exp(-Fans(Ag, YrNum) - M)
Next Ag
ActiveSheet.Cells(10 + AgeNum, 1 + YrNum + 1) = N(AgeNum, YrNum) * Exp(-Fans(AgeNum, YrNum) - M)
+ N(AgeNum - 1, YrNum) * Exp(-Fans(AgeNum - 1, YrNum) - M)

'翌年の加入重量(t)
For Ag = 2 To AgeNum - 1
    ActiveSheet.Cells(10 + AgeNum + 2 + Ag, 1 + YrNum + 1) = N(Ag - 1, YrNum) * Exp(-Fans(Ag, YrNum)
    - M) * aveW(Ag)
Next Ag
ActiveSheet.Cells(10 + AgeNum + 2 + AgeNum, 1 + YrNum + 1) = (N(AgeNum, YrNum) * Exp(-Fans(AgeNum,
YrNum) - M) + N(AgeNum - 1, YrNum) * Exp(-Fans(AgeNum - 1, YrNum) - M)) * aveW(AgeNum)

For CdataNum = 1 To qNum
    ActiveSheet.Cells(9 + (7 + AgeNum * 2) * (1 + CdataNum), 1) = "q-" & CdataNum
    ActiveSheet.Cells(9 + (7 + AgeNum * 2) * (1 + CdataNum), 2) = q(CdataNum)
    For Yr = 1 To YrNum
    'CPUE 表示
        ActiveSheet.Cells(12 + AgeNum + (7 + AgeNum * 2) * (1 + CdataNum), Yr + 1) = LnCPUE(Yr,
        CdataNum)
        ActiveSheet.Cells(12 + AgeNum + (7 + AgeNum * 2) * (1 + CdataNum), 1) = "LnCPUE Obs."
        ActiveSheet.Cells(13 + AgeNum + (7 + AgeNum * 2) * (1 + CdataNum), Yr + 1) = Log(q(CdataNum)
        * SN(Yr, CdataNum))
        ActiveSheet.Cells(13 + AgeNum + (7 + AgeNum * 2) * (1 + CdataNum), 1) = "LnCPUE Est."
    Next Yr
        ActiveSheet.Cells(7, 1 + CdataNum) = "q-" & CdataNum
        ActiveSheet.Cells(8, 1 + CdataNum) = q(CdataNum)
Next CdataNum
```

```
        ActiveSheet.Cells(7, 1) = "SSQ"
        ActiveSheet.Cells(8, 1) = ssq
Return


Retros:
    For Yr = 1 To YrNum
        For Ag = 1 To AgeNum
            nsum = nsum + N(Ag, Yr) * aveW(Ag)      'N の出力(重量(t))
            ActiveSheet.Cells(33 + retro, 1 + Yr) = nsum
        Next Ag
        nsum = 0
    Next Yr

    YrNum = YrNum - 1       'レトロスペクティブ解析で年をさかのぼるので, ここで年数を減らす
Return

'#MENU#

'ブートストラップ リサンプリング データ作成 cpue
'ブートストラップデータ入力 catch
'ブートストラップデータ入力 cpue
'ブートストラップ計算結果出力


'****************************************
'*                                      *
'*  Bootstrap サンプル作成  CPUE data    *
'*                                      *
'****************************************
BootSample_CPUE:
Worksheets("bootstrap_data").Activate

    For CdataNum = 1 To qNum
        For Yr = 1 To YrNum
        '漁法別標準偏差計算 パラメトリック法
            CPUEse(CdataNum) = CPUEse(CdataNum) + (LnCPUE(Yr, CdataNum) - Log(q(CdataNum) * SN(Yr,
            CdataNum))) ^ 2
        Next Yr
        CPUEse(CdataNum) = (CPUEse(CdataNum) / YrNum) ^ 0.5
    Next CdataNum

    For bt = 1 To bootNum
        For CdataNum = 1 To qNum
            For Yr = 1 To YrNum
                ActiveSheet.Cells(1, 1 + Yr + (YrNum + 1) * (CdataNum - 1)) = StartYear + Yr - 1     '年の
                出力
                'LnCPUE の Bootstrap sample(理論値+標準偏差*正規乱数)
                ActiveSheet.Cells(1 + bt, 1 + Yr + (YrNum + 1) * (CdataNum - 1)) = Log(q(CdataNum) * SN(Yr,
                CdataNum)) + CPUEse(CdataNum) * (-2 * Log(Rnd)) ^ 0.5 * Cos(2 * 3.1415926535 * Rnd)
                ActiveSheet.Cells(1 + bt, 1 + (YrNum + 1) * (CdataNum - 1)) = "LnCPUE-" & CdataNum & "-"
                & bt          'LnCPUE 出力
            Next Yr
        Next CdataNum
    Next bt

    For Ag = 1 To AgeNum
        For Yr = 1 To YrNum
            For CdataNum = 1 To CatchNum
```

```
            '行ラベル表示
            ActiveSheet.Cells(1, (YrNum + 1) * CatchNum + 5 + (CdataNum - 1) * (YrNum * AgeNum + 1) + Yr
            * AgeNum + Ag) = StartYear + Yr - 1 & "-" & Ag & " Catch-" & CdataNum
            Next CdataNum
        Next Yr
    Next Ag
Return


'*************************************
'*                                   *
'*     Bootstrap DATA INPUT (Catch)      *
'*                                   *
'*************************************
BootDataInput_Catch:
Worksheets("bootstrap_data").Activate

    For Yr = 1 To YrNum
        For Ag = 1 To AgeNum
            Csum(Ag, Yr) = 0
        Next Ag
    Next Yr

    For CdataNum = 1 To CatchNum
        For Yr = 1 To YrNum
            For Ag = 1 To AgeNum
                'Catch data input
                C(Ag, Yr, CdataNum) = ActiveSheet.Cells(1 + bt, (YrNum + 1) * CatchNum + 5 + (CdataNum -
                1) * (YrNum * AgeNum + 1) + Yr * AgeNum + Ag)
                Csum(Ag, Yr) = Csum(Ag, Yr) + C(Ag, Yr, CdataNum)
            Next Ag
        Next Yr
    Next CdataNum

    'ブートストラップ CATCH データ入力
Return


'*************************************
'*                                   *
'*      Bootstrap DATA INPUT (CPUE)      *
'*                                   *
'*************************************
BootDataInput_CPUE:

Worksheets("bootstrap_data").Activate
    'ブートストラップ CPUE データ入力
    For CdataNum = 1 To qNum
        For Yr = 1 To YrNum
            LnCPUE(Yr, CdataNum) = ActiveSheet.Cells(1 + bt, 1 + Yr + (YrNum + 1) * (CdataNum - 1))
        Next Yr
    Next CdataNum
    'ブートストラップ CPUE データ入力
Return


'*****************************
'*                           *
'*    ブートストラップ結果表示      *
```

```
'*                              *
'*****************************
BootOutPut:
Worksheets("BootstrapResult").Activate

    ActiveSheet.Cells(10 + bt, 1) = bt
    ActiveSheet.Cells(10 + bt, 2) = ssq

    For i = 1 To paraNum
        ActiveSheet.Cells(10 + bt, 2 + i) = (x(1, i))
    Next i

    '資源尾数(尾)・(年)の出力
    For Yr = 1 To YrNum
        For Ag = 1 To AgeNum
            Nyear = Nyear + N(Ag, Yr)
        Next Ag
        ActiveSheet.Cells(10, (4 + CatchNum) + Yr) = StartYear + Yr - 1 & "(尾)"     '年の出力 資源尾数
        ActiveSheet.Cells(10 + bt, (4 + CatchNum) + Yr) = Nyear
        Nyear = 0
    Next Yr
    'YrNum(最終年)の資源尾数(尾)
    For Ag = 1 To AgeNum
        ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + Ag) = StartYear + YrNum - 1 & "-" & Ag &
        "(尾)"
        ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + Ag) = N(Ag, YrNum)
    Next Ag

    '翌年の加入尾数
    For Ag = 2 To AgeNum - 1 '2 歳から最高齢-1 歳まで
        ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (Ag - 1)) = StartYear + YrNum
        & "-" & Ag & "(尾)"
        ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (Ag - 1)) = N(Ag - 1,
        YrNum) * Exp(-Fans(Ag, YrNum) - M)
        Nyear = Nyear + N(Ag - 1, YrNum) * Exp(-Fans(Ag, YrNum) - M)
    Next Ag
    '翌年 最高年齢 資源尾数計算
    ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum - 1)) = StartYear + YrNum
    & "-" & AgeNum & "(尾)"
    ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum - 1)) = N(AgeNum,
    YrNum) * Exp(-Fans(AgeNum, YrNum) - M) + N(AgeNum - 1, YrNum) * Exp(-Fans(AgeNum - 1, YrNum) -
    M)
    '翌年 総資源尾数
    ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + AgeNum) = StartYear + YrNum &
    "-Sum" & "(尾)"
    ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + AgeNum) = Nyear + N(AgeNum,
    YrNum) * Exp(-Fans(AgeNum, YrNum) - M) + N(AgeNum - 1, YrNum) * Exp(-Fans(AgeNum - 1, YrNum) -
    M)
    Nyear = 0

    '資源重量(t)・(年)の出力
    For Yr = 1 To YrNum
        For Ag = 1 To AgeNum
            Nyear = Nyear + N(Ag, Yr) * aveW(Ag)
        Next Ag
        ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + Yr) = StartYear
        + Yr - 1 & "(t)"     '年の出力 資源重量
        ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + Yr) = Nyear
        Nyear = 0
```

```
    Next Yr

    For Ag = 1 To AgeNum
        ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + (YrNum + 2) +
        Ag) = StartYear + YrNum - 1 & "-" & Ag & "(t)"
        ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + (YrNum +
        2) + Ag) = N(Ag, YrNum) * aveW(Ag)
    Next Ag

    '翌年の加入重量
    For Ag = 2 To AgeNum - 1        '2 歳から最高齢-1 歳まで
        ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + (YrNum + 2) +
        (AgeNum + 2) + (Ag - 1)) = StartYear + YrNum & "-" & Ag & "(t)"
        ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + (YrNum +
        2) + (AgeNum + 2) + (Ag - 1)) = N(Ag - 1, YrNum) * Exp(-Fans(Ag, YrNum) - M) * aveW(Ag)
        Nyear = Nyear + N(Ag - 1, YrNum) * Exp(-Fans(Ag, YrNum) - M) * aveW(Ag)
    Next Ag
    '翌年 最高年齢 資源重量(t)計算
    ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + (YrNum + 2) +
    (AgeNum + 2) + (AgeNum - 1)) = StartYear + YrNum & "-" & AgeNum & "(t)"
    ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + (YrNum + 2) +
    (AgeNum + 2) + (AgeNum - 1)) = (N(AgeNum, YrNum) * Exp(-Fans(AgeNum, YrNum) - M) + N(AgeNum - 1,
    YrNum) * Exp(-Fans(AgeNum - 1, YrNum) - M)) * aveW(Ag)
    '翌年 総資源重量(t)計算
    ActiveSheet.Cells(10, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + (YrNum + 2) +
    (AgeNum + 2) + AgeNum) = StartYear + YrNum & "-Sum" & "(t)"
    ActiveSheet.Cells(10 + bt, (4 + CatchNum) + (YrNum + 2) + (AgeNum + 2) + (AgeNum + 2) + (YrNum + 2) +
    (AgeNum + 2) + AgeNum) = Nyear + (N(AgeNum, YrNum) * Exp(-Fans(AgeNum, YrNum) - M) + N(AgeNum -
    1, YrNum) * Exp(-Fans(AgeNum - 1, YrNum) - M)) * aveW(Ag)
    Nyear = 0
Return
End Sub
```

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和文要旨

魚類におけるビタミンKの分布と生理機能に関する研究

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本研究では魚類におけるビタミンKの分布を調べると共に，生体内における生理機能について考察を行った。魚類の組織中にはビタミンKが含まれるが，その量と種類は魚種や食性により大きく異なることがわかった。生体内中のビタミンKの中でフィロキノンは大量に見いだされたが，メナキノン類は少量であった。また，ビタミンKの吸収率はフィロキノンで高く，メナキノン類で低くなっており，魚類のビタミンK利用能については両者で異なる可能性が示唆された。魚類をビタミンK欠乏食で飼育すると，産卵期においては死亡が多発すること，仔魚期においては骨異常個体が増加すること等も明らかになった。この増加は卵中及び餌中にビタミンKが欠乏したときに顕著であり，骨組織が薄く脆弱になる様子が観察された。これにより，ビタミンKは魚類にとって必須の成分であり，特に骨の発達に大きな役割を果たしていることが判明した。

No.18，1-40（2006）

本州東方海域におけるツノナシオキアミの漁業及び生活史に関する研究

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ツノナシオキアミは北太平洋における優占するオキアミ類であり，本邦太平洋側ではオホーツク海南西部から駿河湾にかけて分布している。本種は冬春季の三陸・常磐沿岸において重要な漁獲対象種である。1992～2001年の年間平均漁獲量，漁獲金額はそれぞれ6万6千トン，31億円である。年間漁獲量，漁期及び漁獲金額の年変動は大きいため，安定した経営及び流通のため正確な資源量の評価及び漁況予測が求められている。一方，本種は，多くの固有種，回遊種の重要な餌となり，生態系における鍵種である。また，その大きな生物量を考慮すると，低次生産に対する捕食圧も大きなものと推察される。このように，本種が北太平洋において低次栄養段階から高次栄養段階への物質の輸送に重要な役割を果たしていることを考慮すると，海洋生態系の構造を理解するうえで，本種の分布，生活史及び炭素収支に関する定性・定量的な研究が重要となる。そこで，本研究では本州東方域における本種の漁業，水平・鉛直分布，生活史，生物量，炭素収支（生産量及び代謝量），食性を検討した。

まず，海況変動がツノナシオキアミの漁況にどのように影響してきたか明らかにするために，本漁業の発展や漁獲規制を考慮しつつ，単位努力当り漁獲量（CPUE）等の漁況指数の経年変化を親潮第一分枝等の海況指数との関係で調べた。その結果，漁況と海況の関係では次のような傾向が認められた。すなわち，親潮第一分枝の南下が弱い年には，漁況は岩手県沿岸域では比較的安定するが，宮城県沿岸域及び常磐沿岸域では低いCPUEを示したり初漁日が遅くなったりして不漁を呈した。一方，親潮第一分枝の南下が強い年には，宮城県沿岸域及び常磐沿岸域では岩手県沿岸域と同様に高いCPUEを示したり初漁日が早くなったりして好漁を呈した。

本州東方域におけるツノナシオキアミの水平分布及び生活史の平均像を明らかにするために，ノルパックネットと新稚魚ネットを用いて広域（約36－43°N，145°E以西）における本種の産卵域，分布，成長の季節変化及び寿命を調べた。その結果，交尾と産卵は周年親潮域と親潮系冷水域で行われ，春季にその盛期を迎え，晩秋～冬季に停滞気味であった。成長については，小型成体（越冬前）において3～6月に明確な成長が認められた。寿命は，雄で24ヶ月，雌で28ヶ月と推定された。発育段階間の分布については，ファーシリア期から成体にかけて徐々に冷水域側に分布を拡げる一方，大型成体（越冬個体）で暖水域側に出現しなくなる傾向が認められた。また，産卵域や各発育段階の地理的な分布パターンは季節的な水塊の配置と密接な関係を有した。

ツノナシオキアミの鉛直分布の実態及びそれを規定する物理・生物的環境要因を明らかにするため，ORI，ビームトロール，MOCNESSネット標本を用いて本州東方域の三陸沿岸域（陸棚及び陸棚斜面上部）及び沖合域における本種の鉛直分布の季節変化を調べた。まず三陸沿岸域では，水温躍層が発達し近底層に8℃未満の冷水が存在する6～12月の陸棚斜面上部に本種の底付群が形成されていた。しかし，春季には全水柱をほぼ7－8℃で覆われる陸棚域で漂泳群が多く出現し，底付群は全沿岸域においてほとんど認められなかった。沖合域では，全測点平均でみると，夜間の分布深度（中央値）はファーシリア中期から大型成体にかけて発育するにつれて徐々に深くなる傾向が認められた。一方，昼間の分布深度はファーシリアⅠ期から同Ⅵ期にかけて発育するにつれて徐々に深くなる傾向が認められた。夏～秋季の暖水域における夜間の未成体及び成体の分布深度は深くなる傾向が認められ，特に大型成体は中層の躍層より上部をほとんど超えることができなかった。一方，春季の日中の未成体及び成体の分布深度は夏～秋季（300－400m）に比べ浅く（約150m），その結果鉛直幅の短くなる傾向が認められた。

ツノナシオキアミの炭素収支の特徴を明らかにするため，道東～常磐沿岸域における本種の生物量，生産量及び代謝量を調べた。生物量は，道東域では夏～秋季，三陸・常磐域では晩春～初夏に高かった。年平均生物量は，道東，三陸，常磐域でそれぞれ381，314，258mg C m^{-2}であった。ほぼ年間の全生産量（成長＋脱皮＋産卵）は，道東域（3,829mg C m^{-2}）と三陸域（3,872mg C m^{-2}）で同様であったが，両海域とも常磐域（2,243mg C m^{-2}）より顕著に高かった。各海域において成長生産量が全生産量の占める割合（51.5－70.9%）が最も高かった。全代謝量（基礎代謝＋鉛直移動による代謝）は3,062～3,486mg C m^{-2}で，同化量（全生産量＋全代謝量）の50.1－57.7% を占めた。このうち，基礎代謝量（2,257～2,783mg C m^{-2}）は同化量の32.8－42.5% と，各海域とも最も高い割合を占めた。

環境中の餌生物に応じてツノナシオキアミ成体の食性や摂餌様式がどのように変化するか明らかにするため，道東域及び常磐域における本種の胃内容物の季節変化を調べた。ツノナシオキアミは，環境中のクロロフィル *a* 濃度が高い時に多くの珪藻を摂餌し，クロロフィル *a* が低い時にカイアシ類を摂餌する傾向が認められた。一般に，胃内容中のカイアシ類の個体数及び炭素量とも常磐域の方が道東域より高かった。全摂餌量に対するカイアシ類の割合は道東域で7.3%，常磐域で30% と推定され，緯度の低い温暖な海域ほどカイアシ類の餌としての重要性が高まると考えられた。

以上得られた結果をもとに，同属の南極オキアミや *Neocalanus* 属のカイアシ類と比較しながら，ツノナシオキアミの季節的回遊の重要性，三陸・常磐沿岸域における本種の漁場形成機構，本種の摂餌が低次生産に与える影響について論議した。

No.18，41-165（2006）

伊豆諸島北部海域におけるタカベの資源学的研究

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タカベ *Labracoglossa argentiventris* は，九州から房総半島にいたる太平洋岸の岩礁域に生息し，伊豆諸島の沿岸漁業において多く漁獲される。伊豆諸島北部海域において年間の魚種別水揚げ重量，金額ともに1位の主要漁獲物であり，当資源の持続的利用を確保することは，地域の水産業においても重要な課題である。本研究はタカベの年齢や成長，単位努力量あたり漁獲量（CPUE）の標準化，資源量推定などの資源学的研究により，資源の現状評価や資源管理に必要な基礎的情報を得ることを目的とする。

第二章は，従来年齢査定に使用されていなかった耳石について，年齢形質としての有効性を検証した。伊豆大島周辺海域で収集したタカベの耳石の不透明帯の外縁を輪紋とし，縁辺成長率と縁辺部の輪紋出現割合を調べた。輪紋は，生後1年半の春から夏にかけて第1輪が形成され，その後1年に1本ずつ同時期に形成されると判断した。

第三章は，1994～2003年に伊豆諸島北部海域で収集した標本を用いて，年齢，成長，成熟について調べた。耳石と鱗の輪紋を計測し輪紋数組成を求めた。輪紋数の出現頻度を比較した結果，耳石より鱗の輪紋数が過小に推定される傾向があった。また，耳石と鱗の読み取り誤差を比較した結果，査定値の精度は耳石の方が高かった。

成長を把握するため，年齢－尾叉長関係の von Bertalanffy 成長式と，尾叉長－体重関係のアロメトリー式を推定した。小型魚のサンプルが不十分であったため，全てのパラメータを地区別に推定することは出来なかったが，赤池情報量規準（AIC）より極限体長と分散を大島，利島～式根島，神津島の地区別と性別に，成長係数を性別に推定したモデルが選択された。成長は生後2歳頃まで急速に進み，雄より雌が，また伊豆諸島北部海域で南側の島ほど大型に育つことが示された。耳石と鱗の年齢査定値の違いが成長曲線に与える影響を検討したが，1歳まで体長組成から年齢査定が可能なことに加え，高齢になると成長が緩やかになり年齢と尾叉長の関係があまり変化しないため，推定される成長曲線はほとんど同じであった。アロメトリー式は AIC より，性別に推定した乗法誤差構造のモデルが選択された。生殖腺指数（GSI）の値は，産卵期の9～12月にかけて他の時期より高く，ピークが10月に現れた。同時期の成熟率は，満1歳で15%，満2歳以上でほぼ100% だった。

第四章は，CPUE に含まれる年変動以外の要因を取り除き，資源量指数としての信頼性を高めるため，一般化線形モデルを使用し標準化を行った。1991～2003年の大島の刺網，新島の寄網，神津島の建切網の水揚伝票と，水温と黒潮流路の情報を収集した。島間の移動に関して，伊豆諸島北部海域全体で移動がある場合と，大島，利島～式根島，神津島の地区内でのみ移動がある場合の2つの仮説を考えた。年，月，場所，島と漁法，黒潮流路の接近，黒潮の型，水温の主効果と二次の交互作用を使用し，それぞれの地区について，年の主効果を含む全ての組合せのモデルを推定し AIC の値を比較した。AIC が最小だったモデルは，最小二乗平均を使用し，他の効果を平均化して年変動を抽出した。1991年以降タカベの資源水準は横ばいであっ

た。

第五章は，年齢，漁獲量，CPUE の情報を使用し，移動に関する２つの仮説に基づき，資源量をチューニング VPA で推定した。第三章と飼育魚の知見より，耳石の方が鱗より真の年齢を当てる確率が高く，読み取り誤差が小さいことから，年別年齢別漁獲尾数を求める際，耳石の年齢が正しいと考え，鱗の年齢組成の偏りを耳石の基準に変換した。チューニングには，第四章で標準化した CPUE を使用し，最小二乗法でパラメータを推定した。さらに，CPUE の観測誤差と年齢査定誤差が，パラメータと資源量推定値に与える影響を評価した。1998年以降のタカベの資源量は600～700t 台を推移し，漁獲割合は２～３割だった。資源量推定値の誤差は，近年になると増大する傾向があり，2003年の変動係数は0.2程度だった。また，年齢別の選択率を調べた結果，高齢魚に対して若齢魚の漁獲圧が低いことが示された。これは，価格の高い大型魚を中心に漁獲するため，小型魚の漁獲が抑制されているものと考えられる。推定結果には，島間の移動の仮説による差がほとんどなく，資源管理方策の検討について同様の判断が可能と考えられる。%SPR は2003年の漁獲圧で約50％だった。YPR 解析の結果，漁獲圧を現状より高めた場合，全体の漁獲量はわずかに増加するものの，大型魚の漁獲量は減少することが示唆された。

漁獲係数が $F_{0.1}$ に近いことや，年齢と漁獲の関係，YPR，SPR 解析の結果から判断すると，伊豆諸島北部海域のタカベ資源は漁獲過剰ではないと考えられる。タカベ資源の持続的利用のためには，現状の努力量水準と若齢魚に対する低い漁獲圧の両方を維持する必要がある。

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CONTENTS

Doctoral Thesis

Studies on the Distribution and Physiological Function of Vitamin K in Fish
Miho UDAGAWA 1

Studies on fisheries and life history of *Euphausia pacifica* HANSEN off northeastern Japan
Kenji TAKI 41

A study on the population dynamics of yellowstriped butterfish in the waters around the northern part of the Izu Islands
Shingo WATARI 167

Abstracts (JAPANESE) 243